BREEDING ECOLOGY OF WHITE-WINGED SCOTERS ON THE YUKON FLATS,

ALASKA

By

David Elliot Safine

RECOMMENDED: _____

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Advisory Committee Chair

_____
Chair, Department of Biology and Wildlife

APPROVED: _____
Dean, College of Natural Science and Mathematics

_____
Dean of the Graduate School

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Date

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ALASKA

A

THESIS

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David Elliot Safine, B. S.

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ABSTRACT

Breeding bird surveys indicate a long-term decline in the numbers of scoters (*Melanitta sp.*) in North America. My objectives were to estimate survival of nests, ducklings, and adult female White-winged Scoters (*Melanitta fusca*) breeding on the Yukon Flats National Wildlife Refuge, Alaska, 2002 – 2004, within their primary breeding range. I measured habitat variables at nest sites and random sites in the study area to characterize nest habitat selection, and investigated breeding incidence with a laboratory analysis of circulating concentrations of the plasma yolk precursors vitellogenin (VTG) and very-low density lipoprotein (VLDL). The low hen and nest survival rates I observed combined with the substantial proportion of non-breeders on the breeding ground (up to 28%) may be responsible for the observed declines in abundance if annual survival rates are not high enough to maintain stable populations. Scoters avoided nesting in graminoid habitat, but nested in all other scrub or forested plant communities in proportion to their availability, selecting sites with more cover, higher variability of cover, and closer to edge and water than random sites. At the nest habitat scale, scoters are generalists, which may reduce the foraging efficiency of nest predators.

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PREFACE

This thesis is dedicated to the memories of my father, Stuart A. Safine, and grandfather, Harry H. Eisenberg, who passed away during the final year of my graduate program. Both of these men taught me the value of critical thinking and hard work, two skills necessary to complete my graduate studies. I would also like to dedicate this thesis to my mother, Bonnie E. Safine, for all her encouragement and love over the years. I would not have gotten this far without you.

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INTRODUCTION

Life history theory predicts trade-offs between survival and reproduction because increased fecundity is assumed to decrease survival rate (Cam et al. 1998). Because individuals cannot simultaneously increase both survival and reproduction, organisms select reproductive strategies which maximize their lifetime reproductive success. A wide variety of life history strategies can be seen among North American waterfowl. Swans (Tribe Cygnini) are long-lived, with delayed maturation, small clutch sizes, bi-parental care, and long periods required for incubation and fledging of young (Bellrose 1980). Dabbling ducks (Tribe Anatini) have a shorter life span, reproduction in their first year, large clutch sizes, female-only care of young, and shorter incubation and fledging periods. Sea ducks (Tribe Mergini) are found near the center of this spectrum: some aspects of their life history are similar to those of geese and swans, such as delayed maturation, and some traits are comparable to those of dabbling ducks, like female-only care of young and larger clutch sizes (Bellrose 1980).

Life history strategies also vary within tribes. Most sea ducks adopt one of three basic strategies during the nesting season: coastal ground nesting with little cover, interior ground nesting with dense cover, or cavity nesting. Common Eiders (*Somateria mollisima*) are a good example of the first strategy, nesting in coastal areas, on exposed grassy or sandy locations, often on islands; these are open sites with high potential for nest loss to avian and mammalian predators, but low potential for mortality of breeding females (Goudie et al. 2000). White-winged Scoters (*Melanitta fusca*), take a different

strategy; commonly nesting far inland in areas with dense nesting cover (Brown and Fredrickson 1997). These well concealed nest sites may offer lower rates of nest detection by predators, but are more difficult sites for these heavy bodied birds to escape (Brown and Fredrickson 1989), leading to higher potential hen mortality. Lastly, some sea ducks, like Barrow's Goldeneye (*Bucephala islandica*), have high nest survival probability in deciduous tree cavities (Evans et al. 2002), and the lowest potential mortality of hens; however, the availability of natural cavities is very limited. Numerous studies have been conducted on the breeding ecology of sea ducks with the first (Dau 1974, Coulson 1984, Kellett 1997) and last strategies (Savard 1986, Eadie 1989, Evans et al. 2002), but relatively few studies describe the breeding ecology of sea ducks nesting in the dense cover of inland forests, primarily because nests are difficult to find (Traylor et al. 2004).

Additionally, studies on the breeding ecology of inland nesting sea ducks, such as White-winged Scoters, have not been conducted throughout their breeding range. Studies of White-winged Scoters in North America have focused on island nesting scoters in the prairie-parkland ecotone on the southern end of their breeding distribution (Brown and Brown 1981, Kehoe 1989, Traylor et al. 2004). Management of White-winged Scoters will require knowledge of vital rates from across their range, on both island and mainland sites. Although some White-winged Scoters breed in the Canadian prairies (Bellrose 1980), the majority of the 1.19 million scoters surveyed in North America breed in the northern boreal forest of Canada and Alaska (Canadian Wildlife Service 2004).

Although the boreal forest comprises the majority of the breeding range for White-winged Scoters and some other duck species, such as Lesser Scaup (Austin et al. 1998, Brown and Fredrickson 1997), ecology of scoters and waterfowl generally is poorly described in the boreal forest. However, even though poorly described and relatively undeveloped, the northern boreal forest faces important threats from development projects. Oil and gas development has been proposed for both the Mackenzie Delta (Haszard 2001) and Yukon Flats National Wildlife Refuge (hereafter Yukon Flats; U.S. Fish and Wildlife Service 2005), both important breeding areas. The Yukon Flats in eastern interior Alaska supports one of the densest populations of breeding White-winged Scoters in North America (Bellrose 1980) with over 2.7 individual scoters per km^2 (Conant and Groves 2003). Studies of the breeding ecology of boreal forest birds are valuable to managers who need to develop conservation plans in response to development issues (Haszard 2001).

Of conservation interest, White-winged Scoters are both poorly described in their northern breeding range and declining in numbers. North American surveys of three scoter species, Black (*Melanitta nigra*), Surf (*Melanitta perspicillata*), and White-winged Scoters (*Melanitta fusca*), indicate breeding populations have declined 1.1% per year in areas surveyed since 1961 (Canadian Wildlife Service 2004). The Alaska breeding population of scoters has been stable or gradually declining (-0.4% per year), whereas scoter populations in Western Boreal Canada and Canadian Prairie strata are declining more rapidly (-1.2 and -4.5% per year, respectively) since 1961 (Canadian Wildlife Service 2004). In order to conserve White-winged Scoters on the breeding grounds, an

understanding of both their habitat requirements and reproductive parameters is necessary (Sea Duck Joint Venture Management Board 2001).

Describing nest site selection of boreal White-winged Scoters will bolster our understanding of the life history strategies of ground nesting sea ducks that nest inland. Females should select nest sites to maximize survival of both nests and themselves (Hoekman 2002a), and site characteristics that have been shown to affect survival include: habitat type and layers in the vegetation (Martin 1993, Martin 1995, Crabtree et al. 1989), distance to water and edge (Clark and Shutler 1999, Traylor et al. 2004), and density of cover (Traylor et al. 2004, Badyaev 1995, Clark and Shutler 1999).

Nest site selection as well as other factors affect the vital rates of White-winged Scoters. The estimation of vital rates and their sources of variation is important management goals for declining species. Vital rates often estimated for birds include survival of nests, females, and chicks, clutch size and hatchability, and nesting and renesting probability (Hoekman et al. 2002b). Survival of nests and breeding females was shown to be the most important vital rates in explaining variation in the intrinsic rate of increase (λ) in Mallards (*Anas platyrhynchos*; Hoekman 2002b). Johnson et al. (1992) found that nest and duckling survival and breeding probability were the vital rates most important in determining the reproductive output of Mallards and Wood Ducks (*Aix sponsa*). Estimates of nest and duckling survival are available for White-winged Scoters in the prairie-parklands (Brown and Brown 1981, Traylor et al. 2004, Traylor and Alisauskas 2005), but there are no estimates available for breeding season survival and breeding probability of female scoters. Moreover, there are few estimates of breeding

probability available for waterfowl in general (Johnson et al. 1992, Sedinger et al. 2001).

Most studies estimate breeding probability with mark-recapture data, and assume all

females present on the breeding grounds attempt to nest. The relatively novel approach

to determining laying status with plasma yolk precursors (Challenger et al. 2001, Gorman

et al. 2005) can identify non-breeding females present on the breeding grounds, allowing

researchers to evaluate the "presence equals breeding" assumption.

   The primary objectives of this study were to estimate vital rates and describe

patterns of habitat use for White-winged Scoters on the Yukon Flats National Wildlife

Refuge, Alaska from 2002 – 2004. I investigated nest habitat selection at two scales in

Chapter 1. The larger scale question was whether or not use of habitat types for nesting

on the study area differed from availability of those habitat types, known as third-order

selection (Johnson 1980). The finer scale question addressed fourth-order selection,

(Johnson 1980) in which I compared the characteristics of nest sites and randomly

located points in the same habitat types. In Chapter 2, I estimated the following

reproductive parameters: survival of nests, females, and ducklings to 30 days, as well as

breeding probability using blood plasma chemistry.

   Nearly all of this work was conducted at the Scoter Lake Complex, on the

south-central Yukon Flats. This study site is located approximately 16 km south of

Canvasback Lake, one of the study sites reported in Grand (1995). I continued a tradition

of studying waterfowl on the Yukon Flats, which began with a large scale inventory by

Lensink (1965), followed by studies of wetlands and waterbird ecology (Heglund 1988,

1992), duck nest survival (Grand 1995) and recently a study of breeding scaup (Corcoran

2005). Most studies on the Yukon Flats focused on waterfowl nesting in graminoid and

scrub plant communities, and little information is available for forest-nesting ducks.

White-winged Scoters were noted as one of the most common ducks on the refuge by

Lensink (1965), but due to the secretive nature of their nesting habits, very little was

known about their nest sites or reproductive parameters. With these motivations I set out

to describe the breeding ecology of White-winged Scoters on the Yukon Flats.

NEST HABITAT SELECTION OF WHITE-WINGED SCOTERS ON YUKON FLATS

NATIONAL WILDLIFE REFUGE, ALASKA[1]

Abstract. Breeding bird surveys indicate a long-term decline in the numbers of

White-winged Scoters (*Melanitta fusca*) breeding in North America. Little is known

about the reproductive life history and breeding habitat of White-winged Scoters on their

primary breeding grounds in the boreal forest of Alaska and Northern Canada. We

characterized the selection of nest habitats and attributes within those habitats by

measuring variables at nests and random sites on the Yukon Flats National Wildlife

Refuge, Alaska. Scoters avoided nesting in meadows, but nested in all scrub or forested

habitat types in proportion to their availability. Hens selected sites with more variable

and abundant overhead and lateral cover and sites closer to edge and water than random

sites. Nests of radio-marked hens were farther from water and edge, and in slightly

thicker cover than nests located on foot. Results of this study imply nearly random use of

scrub and forested habitat types within the study area but selective use of attributes within

those habitat types. This generalist approach to nest site selection at a larger scale may

be an adaptive response to reduce detection by nest predators. Scoters often select nest

sites with dense cover far from water, which may increase nest survival. However, these

concealed sites are difficult for heavy-bodied birds to escape, thus hens may be trading

off nest and their own mortality. We provide evidence that nests located on foot may not

be representative of the population of nests at a study site.

Key words: *boreal forest, edge,* Melanitta fusca, *predation, scale.*

INTRODUCTION

White-winged Scoters (*Melanitta fusca*) breed from the Canadian prairies north and west

through the boreal forest of Canada into interior Alaska (Bellrose 1980). The majority of

the 1.19 million scoters surveyed in North America breed in the northern boreal forest of

Canada and Alaska (Canadian Wildlife Service 2004). The Yukon Flats National

Wildlife Refuge (hereafter Yukon Flats) in eastern interior Alaska comprises one of the

densest populations of breeding White-winged Scoters in North America (Bellrose 1980)

with over 2.7 scoters per km^2 (Conant and Groves 2003). North American surveys of

three scoter species (Black (*Melanitta nigra*), Surf (*Melanitta perspicillata*), and White-

winged Scoters) indicate breeding populations have declined 1.1% per year in areas

surveyed since 1961 (Canadian Wildlife Service 2004). The Alaskan population of

breeding scoters has been stable or gradually declining (-0.4% per year, *P*>0.05), whereas

scoter populations in the Western Boreal Canada and Canadian Prairie strata have been

declining more rapidly (-1.2 and -4.5% per year, respectively) since 1961 (Canadian

Wildlife Service 2004).

In North America, studies of breeding White-winged Scoters are almost

exclusively limited to island nesting populations in the prairie-parkland of Saskatchewan

and Alberta (Brown and Brown 1981, Kehoe 1989, Traylor et al. 2004). However, the landscape and plant communities of the prairie parkland, grasslands and agricultural fields interspersed with groves of deciduous trees, are quite different from the northern boreal forest, which is dominated by coniferous trees and includes a much lesser extent of grasslands (Johnson et al. 1995). Nest sites selected in the boreal forest may differ from those used in the southern portion of the breeding range where less forested area is available. Characterizing the breeding habitat of White-winged Scoters in Alaska and Canada is an information need identified by the Sea Duck Joint Venture Management Board (2001) because exploration and development projects in the boreal forest of Alaska and Canada are important threats to scoter breeding habitat. Oil and gas development has been proposed on both the Mackenzie Delta (Haszard 2001) and Yukon Flats (U.S. Fish and Wildlife Service 2005), both important scoter breeding areas. Describing patterns of nest habitat use in the northern boreal forest will provide baseline information important to managers developing future conservation plans (Haszard 2001).

Nest site selection is also important ecologically because nest location (Gloutney and Clark 1997, Filliater et al. 1994, Martin 1993) can affect nest and female survival. Survival of nests and females is an important element of population growth (Hoekman 2002a); thus females should select nest sites to maximize survival of both (Hoekman 2002b). Nest site characteristics that have been shown to affect survival include habitat type and vegetation layers (Martin 1993, Martin 1995, Crabtree et al. 1989), and nests on islands often have higher survival than those on the mainland (Walker et al. 2005, Lokemoen and Woodward 1992). Distance of nests from water and edge (Clark and

Shutler 1999, Traylor et al. 2004), vegetative heterogeneity (Crabtree et al. 1989), and

cover at nest sites (Traylor et al. 2004, Badyaev 1995, Clark and Shutler 1999) have also

been shown to affect nest survival. In previous studies, White-winged Scoters have been

observed nesting far from water, in dense and often thorny shrubs, and on islands (Brown

and Brown 1981, Brown and Fredrickson 1989, and Traylor et al. 2004); following the

general patterns of nest site selection in waterfowl. We believed that scoters in the boreal

forest would select similar sites to those in the prairie-parkland, and thus predicted we

would observe greater vegetative cover and variability, shorter distances to water and

edge, and more scrub plant communities present at scoter nests than at random sites on

the study area.

Quantifying habitat differences between nests and random sites reveals patterns of

habitat use which have improved survival of nests and females over evolutionary time

(Clark and Shutler 1999). Additionally, because selection can be quantified

hierarchically (Johnson 1980), we believed it would be useful to investigate differences

between nests and random sites at multiple scales. The objectives of this study were to

examine patterns of site use for nesting White-winged Scoters in the northern boreal

forest at two spatial scales: First, a comparison of used and available habitat types,

"third-order" selection or the selection of specific habitat components within a home

range (Johnson 1980); and second, a comparison of the site attributes of nests and

random points, "fourth-order" selection or a more specific level of use within that habitat

type (Johnson 1980).

METHODS

STUDY AREA

We collected data from 2002-2004 on the Yukon Flats, located approximately 170 km north of Fairbanks, Alaska (Fig. 1). The Yukon Flats includes approximately 3.5 million hectares along the Yukon River floodplain in east-central Alaska, and encompasses the largest interior wetland basin in Alaska (Heglund 1988). This basin is regarded as an area of major importance under the North American Waterfowl Management Plan (U.S. Fish and Wildlife Service 1986). Based on our assessment of logistics and scoter distributions during the preliminary research in 2002, we chose to study breeding ecology during 2003 and 2004 at the Scoter Lake Complex (N 66° 14', W 146° 23') in south central Yukon Flats. This study site includes a series of relatively large (~ 1.5 km long) inter-connected lakes and boreal forest (taiga) habitat covering approximately 4400 hectares. The forest habitats are dominated by the following tree species: white and black spruce (*Picea glauca* and *P. mariana*, respectively), paper birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). Willow (*Salix sp.*), shrub birch (*Betula glandulosa*), alder (*Alnus sp.*), and immature or stunted forms of the above tree species dominate the scrub habitats. In herbaceous habitats, grasses (e.g. *Calamagrostis sp.* and *Hordeum sp.*), sedges (*Carex sp.*), and emergent plants (e.g. *Typha sp.*, *Scirpus sp.*, and *Nuphar sp.*) predominate. More complete descriptions of the Yukon Flats are found in Lensink (1965) and Heglund (1988 and 1992).

FIELD METHODS

Nest searching. Because White-winged Scoters often nest far from water or in thick

cover (Brown and Brown 1981) we used two different methods to locate nests: foot

searches with the aid of a dog (Kehoe 1989) and tracking of hens marked with radio

transmitters prior to nesting. We captured hens by driving them into floating mist nets

(Kaiser et al. 1995) modified for duck capture, from 31 May to 13 June, 2002-2004. We

outfitted females with prong and suture radio-transmitters (Model A4430, 9 g, Advanced

Telemetry Systems, Isanti, Minnesota; Mauser and Jarvis 1991, Rotella et al. 1993).

Each females was tracked daily from the ground and once or twice weekly from an

airplane until we either found her nest or confirmed her as a failed or non-breeder. If

females were located on water, we attempted to determine their status (paired or not

paired) without flushing them. If on land, we attempted to find the nest without flushing

the female.

On foot, we searched lakeshores, islands, peninsulas, bog perimeters, and areas

within 600 m from water for nests from 8:00 to 16:00 Alaska Daylight Time, from 21

June to 17 July each year. We defined a scoter nest as a depression with either down,

eggs, or contour feathers identified as White-winged or Surf Scoter. We found nests

initiated in the current or previous year, and we included all active, destroyed, and

hatched scoter nests in our sample. We did not locate any nests older than one year, and

we could accurately identify the species of one year-old nests because of the slow

decomposition rate of egg shells and contour feathers that occurs at scoter nests on the

Yukon Flats. We recorded latitude and longitude data for all nests with a compact Global Positioning System (GPS) unit [± 6 m accuracy].

Nest habitat. We entered GPS coordinates of all nests found from 2002 to 2004 into a database and plotted them on Arc View 3.3 (Environmental Systems Research Institute, Redlands, California, USA) geographic information system program. Using the Animal Movement extension (Hooge and Eichenlaub 2000) we drew a minimum convex polygon for the entire sample of nest sites and generated 80 random locations within this polygon. Random sites were spaced at least 200 m apart, with no distance to polygon border restrictions. We excluded random sites that clearly fell in lakes, but visited all sites within 50 m of the mapped lakeshore, as lake levels have changed since the U.S. Geological Survey maps were made in 1956.

We visited all nest and random sites from July 28th to August 14th in 2003 and 2004 to record site characteristics. At each site we recorded; 1. habitat type, 2. edge type, 3. distance to edge, 4. distance to water, 5. overhead cover, and 6. lateral cover. We classified habitat type using the level II categories listed in the Alaska Vegetation Classification (Viereck et al. 1992 and Heglund 1992), defined as the proportion of cover types in a 10 m radius circle centered on the nest or random point. We defined distance to edge as the distance to the nearest change in habitat type (Clark and Shutler 1999 and Clark et al. 1999), and edge type as the habitat type present beyond that change (Clark et al. 1999). We measured distance to water (Clark and Shutler 1999 and Traylor et al. 2004) as the minimum distance to a body of water large enough to appear on infrared photographs of the area. At each site we marked additional points 5 m from the nest or

random location to better characterize the site. In 2003, we visited nests found in 2002 and 2003, and marked four additional points in the cardinal directions around these nests. In 2004, we visited nests located that year and all random points, marking two additional points at random bearings around each site. We reduced additional points (four to two) in 2004 because of the four fold increase in the number of sites to visit that year and because we determined that two additional sites still provided a good representation of the cover at each site. At each of the two (four) outside points, we recorded overhead and lateral cover only (Fig 2.). We measured overhead cover (Clark and Shutler 1999 and Traylor et al. 2004) with a spherical convex crown densiometer placed on the ground, averaged from the four cardinal directions. We measured lateral cover as the average percent obstruction of five white 6.5 cm^2 blocks on a black cardboard square (Clark and Shutler 1999) viewed 2 m from the side with the head at a height of 60 cm taken from the four cardinal directions. Each site was characterized by the average value of overhead and lateral cover measured at the center and outside points. We defined overhead and lateral cover variation as the standard deviation of the three or five measurements of overhead and lateral cover at each site. After visiting all random sites, we needed to increase the sample in rare habitat types (dwarf tree and tall scrub) to be greater than or equal to the number of nests in rare habitat types, so we visited additional random sites in those two habitat types.

STATISTICAL ANALYSIS

Use versus availability. We performed all statistical analyses using SAS software (SAS Institute 1999). We used a Chi-square test of homogeneity (PROC FREQ) to test for equal proportions of nests and random sites in each habitat type because availability was estimated from random sites (Marcum and Loftsgaarden 1980, Thomas and Taylor 1990). We performed the analysis with and without habitat types that were commonly available but rarely used (Thomas and Taylor 1990). We also performed a test of homogeneity on the proportion of edge habitat types at both nest and random sites in habitat types used for nesting. We verified that expected frequencies were greater than one and the average expected frequencies were greater than six to assure appropriateness of the Chi-square test (Zar 1999).

Effects of sampling design and nest searching method. We examined differences in mean cover and variation values collected at nests in 2003 and 2004 (five and three sampling points per site respectively; PROC TTEST) to determine if both protocols provided similar enough results to warrant their combination in the analysis. We also investigated differences in nest site characteristics attributable to the search method (radio telemetry or ground searches with the aid of dogs; PROC TTEST) to understand how method used may affect the regression model.

Site attributes. We used logistic regression (PROC LOGISTIC) to characterize which habitat features affected selection (Alldredge et al. 1998) within habitat types. Our sampling protocol was consistent with a use-availability study as an approximation to a case-control design, which requires the assumption that use of available sites is rare

(Keating and Cherry 2004). Since we were making this rare use assumption, we interpreted the results of logistic regression as odds ratios and not resource selection functions (Keating and Cherry 2004). The explanatory variables used in the models were habitat type, distances to edge and water, lateral and overhead cover, and the variation of lateral and overhead cover. We included 12 additional random points to increase sample size in rare habitat types and achieve a sample of available sites in approximate proportion to use. Because we sampled in proportion to use, we used habitat type just to explain variation in the logistic regression models, but not to infer selection of habitat types themselves. We investigated correlations among explanatory variables with correlation analysis (PROC CORR) and scatter plots. We chose an *a priori* model set of 41 biologically relevant models, and all models with more than two parameters included only additive effects. We used Akaike's Information Criteria (Akaike 1973) adjusted for small sample size (AIC$_c$; Burnham and Anderson 1998) for model selection. We tested goodness-of-fit to the logistic model with the Hosmer and Lemeshow statistic (Hosmer and Lemeshow 1989). Values reported in the results section are means ± SE.

RESULTS

Use versus availability. We visited random sites (*n*=61) in all six terrestrial habitat types: coniferous, deciduous, and mixed forest, dwarf tree and tall scrub, and graminoid herbaceous. We located nests (*n*= 3, 17, and 20 in 2002, 2003, and 2004, respectively) in five of the six terrestrial habitat types on the study area; only graminoid herbaceous

habitat was unused (Table 1). The edge habitat at nests and random points included all

six terrestrial habitats plus water (Table 1). Nests (n=40) and random sites (n=54 without

graminoid sites, n=61 with graminoid points) were present in the same proportions

among the habitat types, whether or not we included the available but avoided graminoid

herbaceous habitat type (without graminoid; χ^2_4 = 4.7, P = 0.32 and with graminoid; χ^2_5 =

9.7, P = 0.08). We found the proportion of edge type at nests (n=39) and random sites

(n=54) to be equal among the seven edge habitat types (χ^2_6 = 6.5, P= 0.37).

Effects of sampling design and nest searching method. There were minimal

differences in mean overhead cover (2% ± 4) and lateral cover (7% ± 5) between nests

with three sampling points (n=19) and five sampling points (n=20). Mean variation in

overhead (0% ± 3) and variation in lateral cover (-2% ± 2) also did not differ between

nests with three sampling points (n=19) and five sampling points (n=20). Sampling

design differences between years will therefore not affect parameter estimates in the

regression model, thus combining sampling designs is warranted. However, mean

distances to water and edge were greater at telemetry nests (+210 m ± 43 and +10 m ± 4,

respectively) than at ground search nests, and there is some evidence that overhead cover

was greater as well (+6 % ± 4).

Site attributes. We included random points (n=50) in the five habitat types that

scoters used for nesting: coniferous, deciduous, and mixed forest; dwarf tree and tall

scrub, and additional points in dwarf tree and tall scrub (n=9 and 3 respectively). Four

random points had water within 5 m and were not included in the analysis. Nests were

closer to edge and water, having denser and more variable cover than random points (Table 2).

The best approximating model in the logistic regression was that site use depends on the additive relationship of all measured variables (distance to edge and water, overhead and lateral cover, the variation in both overhead and lateral cover, and habitat type simplified into two categories, forest or scrub). Five other models were within 7 AICc units, but none were within 2 AIC_c units of the most parsimonious model (Table 3). The top three models were similar, and all included distance effects (edge and water) and cover effects (overhead and lateral). Additionally, the top model included habitat and variation in cover effects, while the next best model added only variation in cover effects. The Hosmer and Lemeshow goodness-of-fit test indicated the most parameterized model fit to the logistic model ($\chi^2_8 = 4.6$, P=0.80). Probabilities predicted by the top model were 85% concordant and 15% discordant with the observed data. Coefficient and odds ratio estimates from the top model (Tables 4 and 5) indicate all variables explain variation in the data with the exception of variation in lateral cover. Distance Coefficients are negative (-0.04 ± 0.02 and 0.00 ± 0.00, edge and water respectively) while overhead (0.09 ± 0.03) and lateral cover (0.05 ± 0.02) and the variation in overhead (0.13 ± 0.05) and lateral cover (0.01 ± 0.04) Coefficients are positive. In the top model, distance to water changes the odds ratio of use much slower than distance to edge (1.00 ± 0.00 and 0.96 ± 0.02, respectively; Fig. 3), and the same relationship is true for the odds ratios of lateral (1.05 ± 0.02) and overhead cover (1.10 ± 0.03; Fig. 4). Overhead cover variation increases the odds ratio of use (1.14 ± 0.05) approximately 100 times over its range,

making its effect size larger than that of lateral cover, but smaller than that of overhead cover (Fig. 5).

The only two variables which were highly correlated were overhead cover and variation in overhead cover ($r = -0.67$, $P < 0.001$). Despite this correlation, the top model (Table 3) which included both overhead cover and the variation in overhead cover fit the data much better than models with one of these parameters missing. The top model without overhead cover included has $\Delta AICc = 7.1$, and the top model without overhead cover variation has $\Delta AICc = 4.5$, suggesting that these correlated variables reduce the deviance enough to warrant their joint presence in the logistic regression models.

DISCUSSION

Use versus availability. Scoters used nesting and edge habitats proportional to their availability. There were no statistically significant differences between use and availability, but there is some biologically meaningful information to be gleaned from this analysis. Of the total Chi-square statistic from the nest habitat analysis, 97% is due to the deviation of the graminoid and dwarf tree scrub observations from their expected values, providing evidence of nesting preference for dwarf tree scrub and avoidance of graminoid habitat. Dwarf tree scrub is rare on the study area, as it normally occurs only in a narrow belt around lakes, which have been drawing down over multiple years, and in bogs. However, 13 % of the nests sites occurred in this habitat type. This cover type was likely selected because it provided dense woody cover relatively close to water and edge.

Graminoid habitats were not rare on the study area (Table 1), but were not used for nesting. Although some nests were located in a graminoid patch, there were always enough trees or shrubs in the 10 m circle around the nest to classify the habitat as forest or scrub. This pattern of little selection among forest and scrub types and avoidance of graminoid habitat showed the importance of woody cover at or near a nest. Scoters selected woody cover without regard to the habitat type in which it occurs. This apparent random use of woody habitat types for nesting may greatly reduce the search efficiency of potential nest predators, reducing the probability that any predator can find scoter nests (Martin 1993). This generalist pattern of site selection may also make it difficult to develop management strategies to minimize the effects of development activities on nesting scoters.

Effects of nest searching method. Search method affected some site characteristics measured at nests, especially distance to water. We searched some areas more intensively than others, particularly those habitats close to edges, shorelines, and islands. The farther we searched from water, the lower our probability of detecting a nest. The same pattern held for distance to edge and increasing overhead cover. Therefore our sample of ground search nests was likely a biased sample of nests on the study area with respect to the site characteristics we measured, whereas we assumed that the sample of nests from radio marked birds would be representative of the population. How could the inclusion of both telemetry and ground search nests in the model affect the results? We may have overestimated the effects of distance to water on site selection; however, we could not quantify the magnitude of this bias. If we had included only

telemetry nests, it is likely that distance to water would no longer explain variation in site use. The effect of distance to edge would decrease if we had included only telemetry nests, but because mean distance to edge only changes +6 m from the mean of all nests (12.3 ± 2.0 m), distance to edge for scoter nests found with telemetry (18.6 ± 4.2 m) would still be lower than the mean value of random sites (29.2 ± 5.3 m); thus this bias would not change the results dramatically. Similarly for overhead cover, the anticipated change would be small, 4% from the overall mean, and the resulting odds ratio curve would be slightly steeper.

Site attributes. White-winged scoters selected nest sites with more cover and variation in cover, and closer to edge and water than random points at the Scoter Lake Complex. Odds of use changed quickly for some parameters in the model over their sampled range, whereas others changed the odds very slowly or not at all. Distance to edge and overhead cover were the parameters we measured with the strongest effects on the odds of use, while overhead cover variation, lateral cover, and distance to water all had moderate to low (respectively) effects on the odds of use (Fig. 3-5).

The odds of use approached zero when distance to edge values were more than 120 m; a negative effect. A negative distance to edge effect was also reported for Ring-necked Pheasants (Clark et al. 1999), and White-winged Scoters nested closer to edge than random sites at Redberry Lake, Saskatchewan (Traylor et al. 2004). In contrast, distance to edge did not differ between nests and unused sites in Wild Turkeys (Badyaev 1995) and in five species of dabbling ducks (Clark and Shutler 1999).

For scoters, distance to edge has important implications for nest and female survival. Being farther from edge may improve nest survival (Clark and Shutler 1999) and at the same time decrease hen survival as hens are farther from the suitable escape cover often present at edges. If edge habitat is lower or more open than the nesting habitat, it may form an opening sufficient for these heavy-bodied birds, with "relatively low and slow take-offs" (Brown and Fredrickson 1989) to fly safely away from approaching nest predators. Such openings are extremely important to the survival of hens, as birds too far from escape cover often succumb to mammalian predators (Safine pers. obs). Furthermore, most nests were within 10 m of an opening suitable for escape, but often this opening is too small to be recorded as a unique edge at the scale used in this analysis.

The odds of use slowly decreased as distance to water increased. Nests were located on average closer to water than random points (142.7 ± 25.5 m and 231.3 ± 22.8 m, respectively), but enough nests were located farther from water than random points (18% of the sample) to produce a gradually declining odds ratio. This pattern is similar to White-winged Scoters in Saskatchewan, which selected nest sites approximately the same distance from water as random points (~107 m; Traylor et al. 2004). Scoters are known to nest long distances from water (Brown and Brown 1981, Bellrose 1980, this study), but what advantage do scoters receive for nesting far from the safety of lakes? Nesting farther from water may improve nest survival enough to offset the potentially negative impacts on females and ducklings during long distance movements to brood rearing habitats. Nesting farther from travel routes of mammalian nest predators, e.g.

shorelines and habitat edges, may improve female and nest survival (Brown and Fredrickson 1989, Paton 1994). Nesting scoters appear to be generalists; individual females place their nests varying distances to water and edge in most habitat types, and then seek thick cover at those sites.

Scoters nested in sites with more overhead and lateral cover than random sites, similar to other waterfowl species (Clark and Shutler 1999, Lokemoen et al. 1984, Traylor et al. 2004). High levels of cover were likely selected by females because they improve nest survival (Traylor et al. 2004, Clark and Shutler 1999, Badyaev 1995). However, while this strategy may reduce detection of the nest, well-concealed sites are more difficult for these heavy-bodied ducks to exit. Therefore, hens need dense cover for the nest site and less dense cover nearby for escape, which could be edge or a small opening. The use of escape cover is likely the reason why overhead cover variation was an important variable in the model, higher levels of which increased the odds of use. On average the three points sampled at random sites tended to be more similar to each other, indicating more uniform cover at random sites. Scoters not only selected for high overhead cover in general, but they chose to place their nests at sites with more heterogeneity in cover.

Scoters selected nest sites from a continuum of available cover densities and distances to water and edge on the Scoter Lake Complex. Placement of nests at various levels along this continuum constitutes different solutions to trade-offs in hen, nest, and brood survival. To improve nest survival, hens may place their nest farther from travel paths of mammalian predators (edges, lakeshores), and in denser cover to obscure

themselves, their eggs, and scent (Martin 1993). Liabilities of this strategy may include decreased hen and duckling survival, due to the lack of suitable escape cover for hens, and long distances to brood rearing areas. On the study area, scoters represent waterfowl at one extreme of the cover and distance continuum, often nesting at sites with very dense cover far from water (D. Safine per. obs.). Thus, we would expect scoters to have the highest nest survival and lowest hen survival during nesting. Dabbling ducks (Tribe Anatini) are in the center of the continuum, and pochards (Tribe Aythyini) on the other extreme, typically nesting in open sites with floating nests or near the water. Because of the open habitat selected by pochards, we expect them to have the lowest nest survival, but highest hen survival during nesting, as females may easily escape from nests. Despite their poor take-off capabilities and longevity, White-winged Scoters at the Scoter Lake Complex often nest at the extreme of the cover and distance continuum, and over the long-term must experience relatively high nest survival compared to dabbling ducks and pochards; otherwise, this strategy would not persist in the species.

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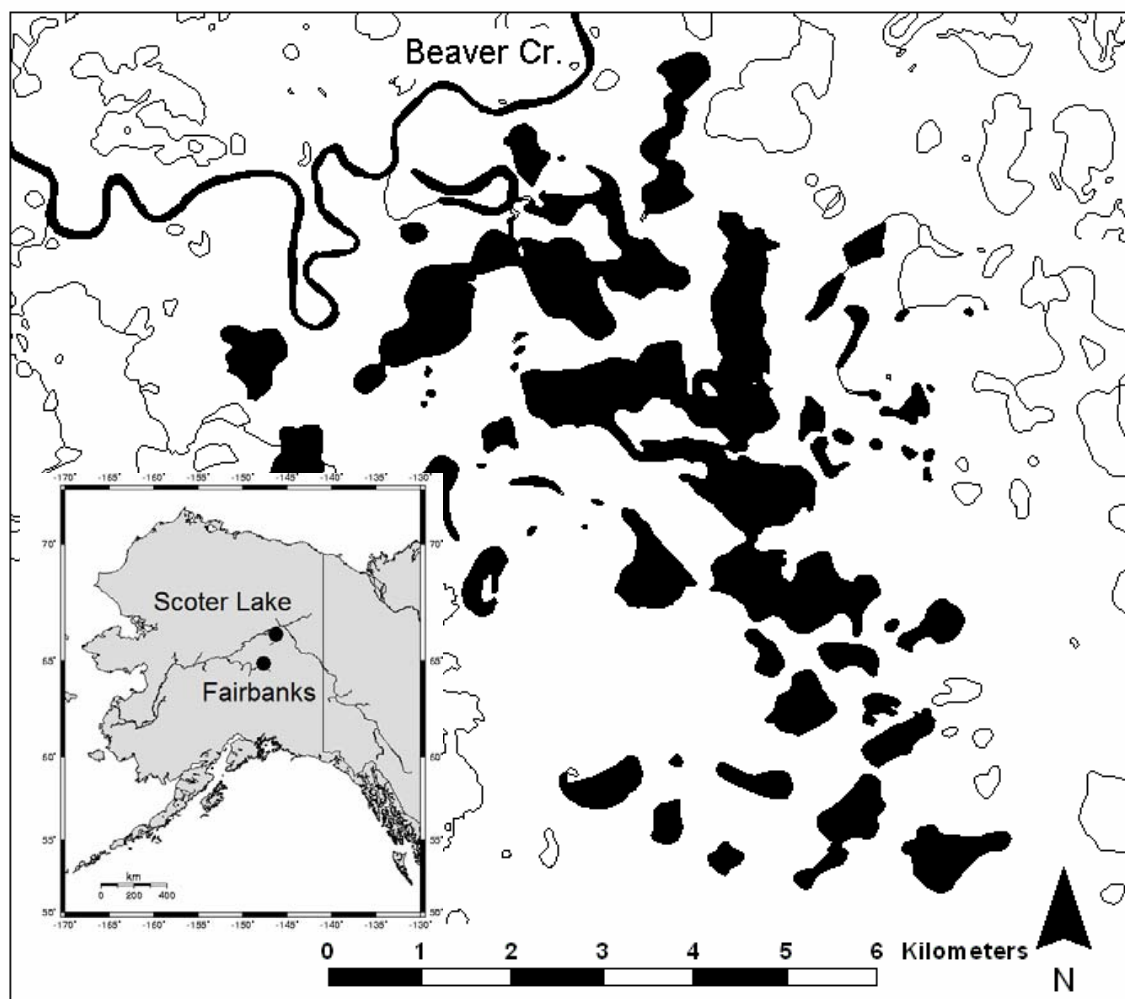
FIGURE 1. Location of the Scoter Lake Complex, south central Yukon Flats National Wildlife Refuge, Alaska. Darkened waterbodies show extent of study area visited from 2002 - 2004.
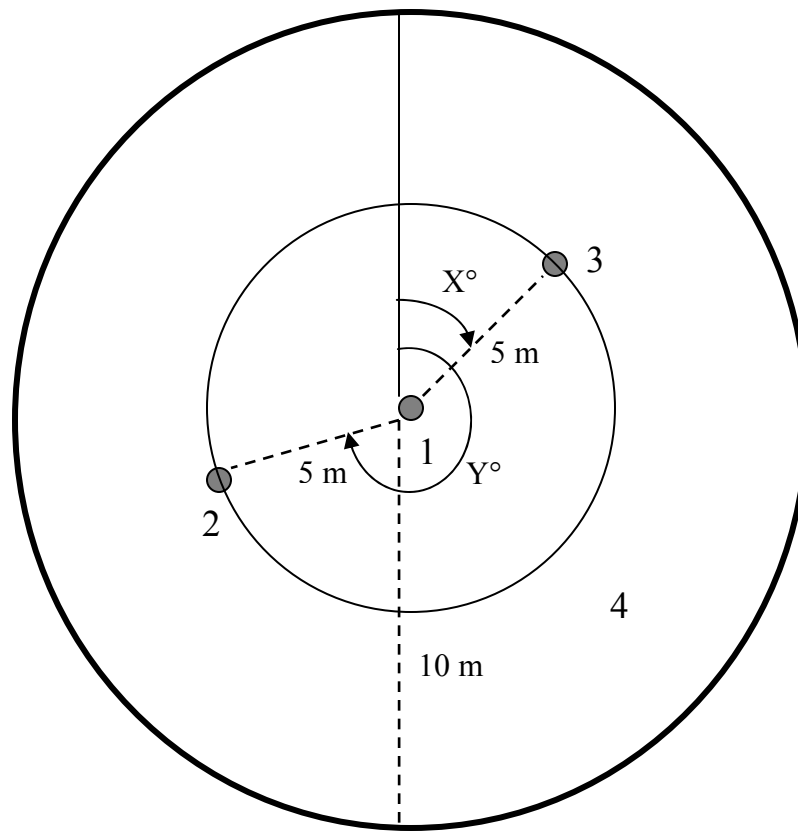
FIGURE 2. Sampling protocol for nests and random points. No. 1 is the nest site or GPS coordinates of the random point. No. 2 and No. 3 are additional sampling points 5 m. from the center. No. 4 is the habitat type of the 20 m. circle around the center point. X and Y are random bearings for the additional points.
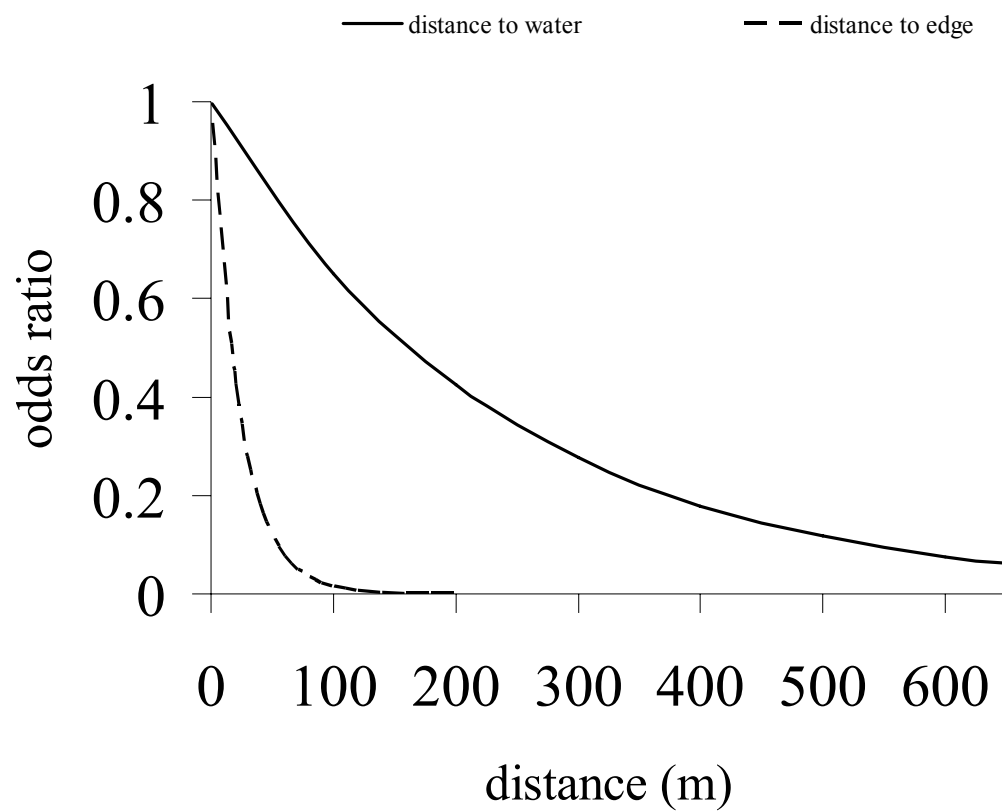
FIGURE 3. Effects of distance to water and edge on the odds ratio of use for breeding White-winged Scoters on the Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2002 - 2004.
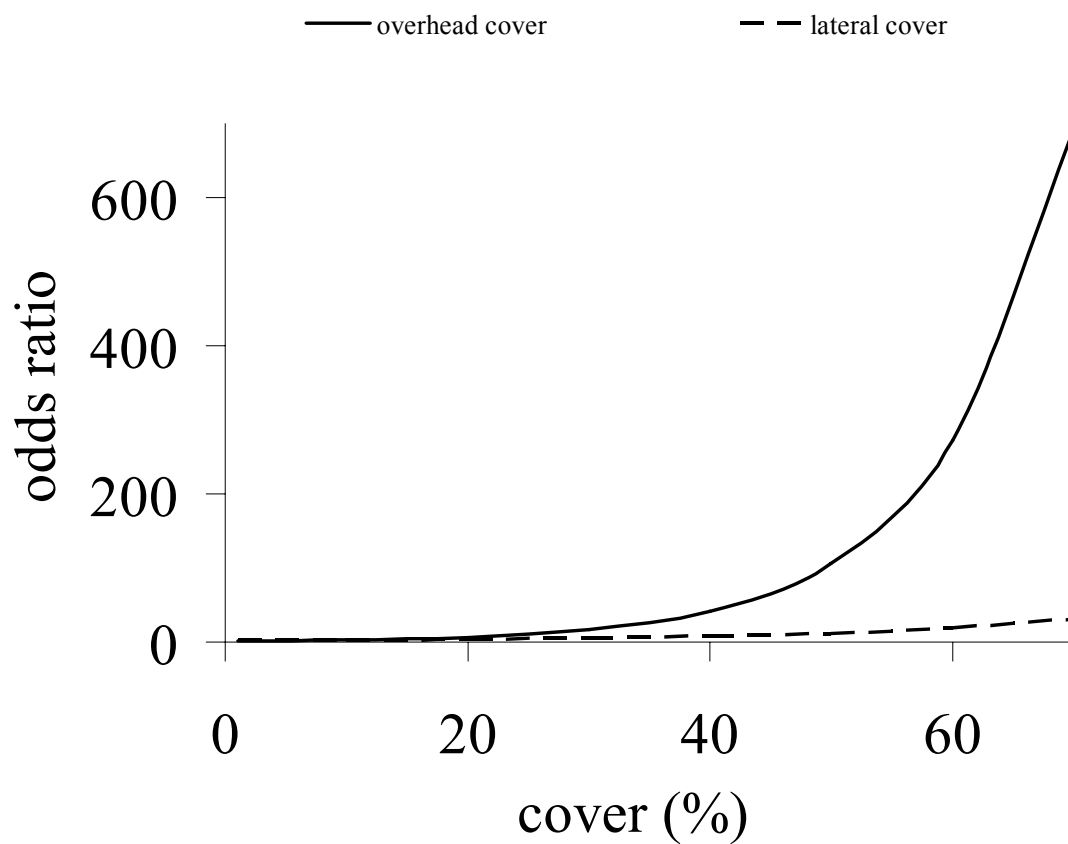
FIGURE 4. Effects of overhead and lateral cover on odds ratio of use for breeding White-winged Scoters on the Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2002 - 2004.
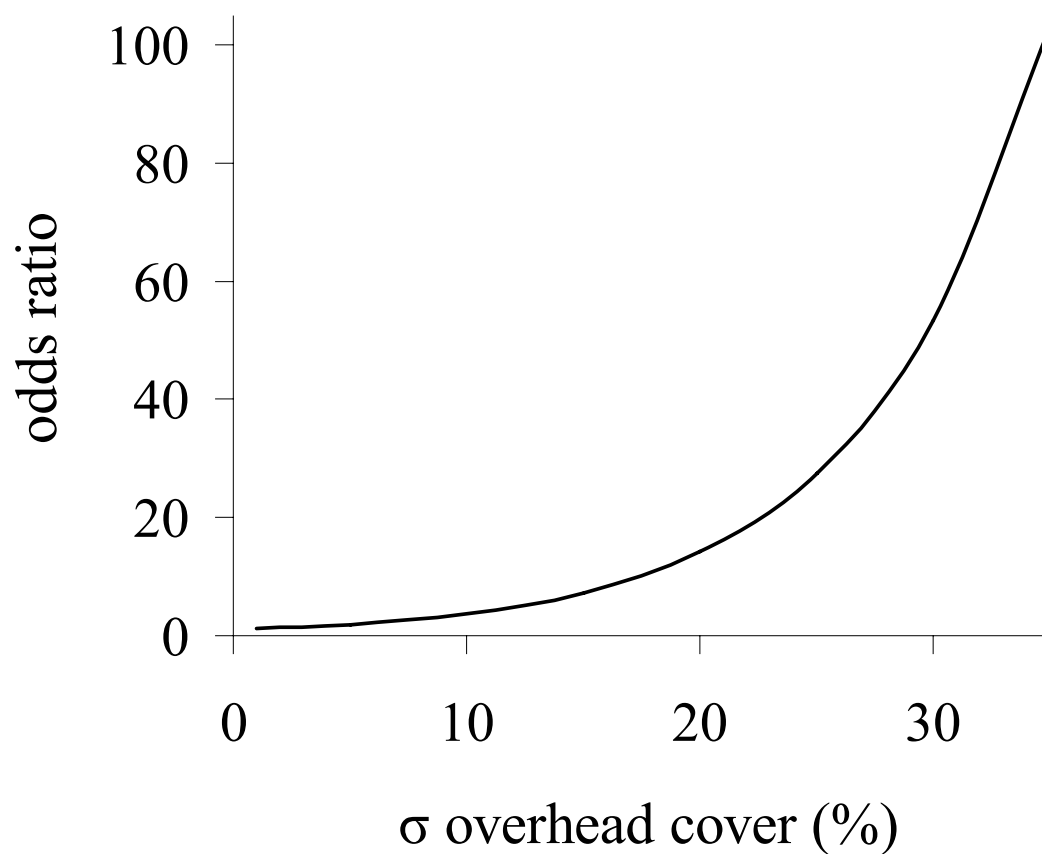
FIGURE 5. Effects of overhead cover variation on odds ratio of use for breeding White-winged Scoters on the Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2002 - 2004.

TABLE 1. Proportion of nests and random points in each habitat and edge type with associated cell chi-square values from the test of homogeneity; Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2002-2004.

	Nests			Random sites		
	n	%	cell χ^2	n	%	cell χ^2
Habitat type						
Coniferous forest	16	40	0.0	26	43	0.0
Deciduous forest	2	5	0.1	4	7	0.0
Mixed forest	13	33	0.1	17	28	0.1
Dwarf tree scrub	5	13	2.9	1	2	1.9
Tall scrub	4	10	0.0	6	10	0.0
Graminoid herbaceous	0	0	2.8	7	12	1.8
Total	40	100	5.9	61	100	3.9
Edge type						
Coniferous forest	7	18	0.2	7	13	0.2
Deciduous forest	3	8	0.2	6	11	0.1
Mixed forest	7	18	0.0	10	19	0.0
Dwarf tree scrub	4	10	0.9	2	4	0.6
Tall scrub	4	10	2.0	15	28	1.4
Graminoid herbaceous	5	13	0.4	4	7	0.3
Water	9	23	0.1	10	19	0.1
Total	39	100	3.8	54	100	2.7

TABLE 2. Means and differences with standard errors for site attributes of nests and random points; Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2002-2004.

Parameter[a]	Nests (n=39)		Random points (n=62)		Difference[b]	SE
	Mean	SE	Mean	SE		
Distance to edge	12.3	2.0	29.2	5.3	-16.9*	6.9
Distance to water	144.3	26.1	240.6	23.3	-96.3*	35.9
Overhead cover	78.9	1.8	73.8	1.9	5.1	2.8
Overhead cover variation	12.1	1.4	11.0	1.0	1.1	1.7
Lateral cover	55.7	2.4	45.1	2.5	10.6*	3.7
Lateral cover variation	16.3	1.2	13.9	1.0	2.4	1.6

[a] Distance is measured in meters, cover as percent obstruction, and variation in cover as standard deviation of percent obstruction.

[b] * indicates P-value < 0.01.

TABLE 3. Model selection results from logistic regression of nest site attributes and location (nest or random point); Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2002-2004. Models are shown with the sources of variation in location, "+" symbols indicating additive relationships among parameters. Number of parameters (k), -2*log likelihood (-2$log(l)$), the difference in Akaike's information criterion, adjusted for small sample size, from the best approximating model (ΔAIC_c), and the coefficient of determination (R^2) are included in the table. We include results from models with $\Delta AIC_c \leq 7$.

Model [a]	k	-2 $log(l)$	ΔAIC_c	R^2
De + Dw + Oc + Ocv + Lc + Lcv + Hab2	8	94.1	0.0	0.33
De + Dw + Oc + Ocv + Lc + Lcv	7	99.2	2.7	0.30
De + Dw + Oc + Lc	5	105.6	4.6	0.25
De + Dw + Oc + Ocv + Lc + Lcv + Hab5	11	92.7	6.0	0.34
De + Dw + Oc	4	110.1	6.9	0.22
De + Dw + Lc	4	110.22	7.0	0.22

[a] Model parameters are distance to edge (De), distance to water (Dw), overhead cover (Oc), overhead cover variation (Ocv), lateral cover (Lc), lateral cover variation (lcv), coarse habitat, habitat type, two classes (Hab2), habitat type, five classes (Hab5).

TABLE 4. Parameter estimates from the logistic regression analysis of site use as a function of site characteristics at Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2002 – 2004.

Parameter[a]	Estimate	95% Confidence Limits[b]		Standardized Estimate[c]
Intercept	-9.72	-16.48	-3.99	
Distance to edge	-0.04	-0.08	-0.01	-0.81
Scrub habitat	-1.60	-3.15	-0.21	
Distance to water	0.00	-0.01	0.00	-0.43
Overhead cover	0.09	0.03	0.16	0.71
Overhead cover variation	0.13	0.03	0.25	0.59
Lateral cover	0.05	0.01	0.09	0.50
Lateral cover variation	0.01	-0.06	0.08	0.03

[a] Beta parameters from the best approximating model.

[b] Profile likelihood confidence interval.

[c] Beta parameters standardized with respect to different measurement units of site attributes.

TABLE 5. Odds ratios estimates and profile likelihood confidence intervals from the top

model of a logistic regression analysis of site use versus site characteristics at Scoter

Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2002 – 2004.

Effect	Odds ratio	Confidence limit	
Distance to edge	0.96	0.92	1.00
Habitat type (scrub/forest)	0.20	0.05	0.87
Distance to water	1.00	0.99	1.00
Overhead cover	1.10	1.03	1.17
Overhead cover variation	1.14	1.03	1.27
Lateral cover	1.05	1.01	1.09
Lateral cover variation	1.01	0.94	1.08

BREEDING ECOLOGY OF WHITE-WINGED SCOTERS ON YUKON FLATS

NATIONAL WILDLIFE REFUGE, ALASKA[1]

Abstract. We studied the reproductive ecology of White-winged Scoters
in one of their primary breeding areas, the boreal forest of Alaska. We captured and
radio- marked 79 paired female White-winged Scoters at the Scoter Lake Complex,
Yukon Flats National Wildlife Refuge, Alaska, in early June 2002-2004. We found nests
(*N*=67) of scoters and other duck species, monitored the fate of 127 scoter ducklings, and
marked additional brood-rearing females (*N*=13) to estimate nest and brood survival.
Blood samples from hens captured in June 2004 were analyzed for levels of the plasma
yolk precursors vitellogenin (VTG) and total very low density lipoprotein (VLDL) to
examine breeding probability. We estimated daily survival rates of hens, nests, and
ducklings and investigated sources of variation in these parameters with generalized
linear models in Program MARK (White and Burnham 1999). Blood assays indicated
that 28% of the paired females we captured in 2004 were not producing eggs, and likely
did not do so subsequently. Summer survival (87-day) was 0.93, 95 % CI (0.75,0.98) and
0.79, 95% CI (0.65, 0.88) for non-egg-producing and egg-producing females,
respectively. Nest survival (28-day) was similar among species and was 0.25, 95% CI
(0.13, 0.49) in forest habitats and 0.03, 95% CI (0.01, 0.16) in graminoid habitats.
Survival probability to 30 days for ducklings hatching on the mean date ranged from

0.01, 95% CI (0.00, 0.05) in 2003 at large wetlands to 0.89, 95% CI (0.80, 1.00) in 2004

at small wetlands. White-winged Scoters at this boreal forest site had lower nest survival,

but higher duckling survival than those nesting in the prairie-parkland; a substantial

proportion of females may not be breeding each year, limiting the potential for population

growth.

Key words: *boreal forest, breeding probability, duckling survival, female*

survival, Melanitta fusca, *nest survival, yolk precursors*

INTRODUCTION

Breeding ecology of waterfowl in the northern boreal forest is poorly understood, and

thus estimates of vital rates from Alaska and northern Canada are generally lacking

(Grand 1995, Brook and Clark 2005). Importantly, for some waterfowl species, the

boreal forest comprises the majority of the breeding range, e.g. Lesser Scaup (*Aythya*

affinis) and White-winged Scoters (*Melanitta fusca*; Austin et al. 1998, Brown and

Fredrickson 1997). Despite its remoteness, important threats to waterfowl breeding

habitat in the northern boreal forest exist in the form of habitat loss due to development

and climate change. Oil and gas development has been proposed on both the Mackenzie

Delta (Haszard 2001) and Yukon Flats (U.S. Fish and Wildlife Service 2005), both

important breeding areas. White-winged Scoters are a species of concern in the boreal

forest and more generally in North America as surveys of three scoter species [(Black

(*Melanitta nigra*), Surf (*Melanitta perspicillata*), and White-winged Scoters] indicate

breeding populations have declined 1.1% per year in areas surveyed since 1961

(Canadian Wildlife Service 2004). Because White-winged Scoters are declining, recent

attention has been focused on which vital rates may be responsible (Sea Duck Joint

Venture Management Board 2001).

Vital rates have been estimated for North American White-winged Scoters in

numerous studies: annual survival (Krementz et al. 1997, Alisauskas et al. 2004), nest

survival (Brown and Brown 1981, Traylor et al. 2004), and duckling survival (Traylor

and Alisauskas 2005) have all been assessed. However, those studies focused exclusively

on island-nesting scoters on the southern end of their breeding distribution. Management

of White-winged Scoters will require knowledge of vital rates from both island and

mainland sites across their range. Additionally, an understanding of the sources of

variation in these vital rates is an important management goal.

Estimating vital rates and describing their sources of variation has been

identified as an important goal, but what vital rates are typically measured, and which of

these has the largest effect on the intrinsic rate of increase (λ)? For birds, the following

vital rates are typically estimated: survival of nests, females, and ducklings, clutch size

and hatchability, and nesting and renesting probability (Hoekman et al. 2002). Hoekman

et al. (2002) estimated that nest and breeding season survival of adult females explained

most (62%) of the variation in λ for Mallards (*Anas platyrhynchos*); duckling survival

was also an important vital rate. Johnson et al. (2002) found that breeding probability

was the third most important vital rate in determining reproductive output, after nest and

duckling survival in Mallards and Wood Ducks (*Aix sponsa*). Some estimates of breeding probability are available for geese, ducks, and sea birds (Sedinger et al. 2001, Anderson et al. 2001, Cam et al. 1998), but there are no estimates available for scoters. Most studies estimate the proportion of the population that attempts to breed each year from mark-recapture data, an approach that often requires the assumption that all birds present on the breeding area attempt to nest (Sedinger et al. 2001, Anderson et al. 2001). These studies often fail to detect non-breeding on the breeding grounds as typically only breeding females are captured or resighted (Yoccoz et al. 2002).

Survival of nests, breeding females, ducklings, and breeding probability are important drivers of population growth rate. Understanding the sources of variation in vital rates gives managers avenues to increase growth rate of declining populations. In studies of nest survival of waterfowl, common sources of variation are day of nesting season, nest age, habitat, species, and abundance of cover (Grand 1995, Walker et al. 2005, Traylor et al. 2004). Studies of duckling and female survival often focus on individual covariates and weather variables such as female body condition, minimum daily temperature, and precipitation (Traylor and Alisauskas 2005, Schmidt et al. 2005) along with some of the same variables found in nest survival analyses. Age of females and wetland conditions have been shown to affect breeding probability in ducks (Anderson et al. 2001, Hoekman et al. 2002), and this vital rate appears to vary tremendously over time (Coulson 1984).

Because scoter populations have declined and estimates of vital rates were lacking, we began a study to estimate demographic parameters, and the factors affecting

those parameters, for a population of White-winged Scoters in the northern boreal forest on the Yukon Flats National Wildlife Refuge, Alaska, between 2002 and 2004. The objectives of this study were to estimate survival of breeding females, nests, and ducklings. For the nest survival portion of the study only, we monitored the fate of nests of scoters and other duck species on the study area. We monitored the nest survival of both scoters and other duck species to provide more precise estimates of both survival probability and sources of variation in survival for White-winged Scoters. Additionally, we investigated breeding probability using physiological measures of plasma chemistry.

METHODS

STUDY AREA

The Yukon Flats, located 170 km north of Fairbanks, Alaska includes a wetland basin of approximately 26,000 km^2 along the Yukon River floodplain in east-central Alaska. This is the largest interior wetland basin in Alaska (Heglund 1988) and is regarded as an area of major importance under the North American Waterfowl Management Plan (U.S. Fish and Wildlife Service 1986). During preliminary research in 2002, we studied scoters at two sites: Plot C (N 66° 23', W 148° 18') on the Western Yukon Flats and the Scoter Lake Complex (N 66° 14', W 146° 23') in South-central Yukon Flats. For the duration of the main study, 2003-2004, we collected data at the Scoter Lake Complex only, and all subsequent description will be of this area. The Scoter Lake study site (Fig. 1) includes a

series of relatively large (~ 1.5 km long) inter-connected lakes as well as smaller isolated

lakes in an approximately 44 km^2 boreal forest study site.

Lensink (1965) noted the complex interspersion of terrestrial habitat types on the

Yukon Flats. Our study area was a good example of that heterogeneity as it included

coniferous, mixed, and deciduous forest, tall and dwarf tree scrub, and graminoid

meadows (Viereck et al. 1992). The wetlands on the study area were also diverse and

attracted a variety of nesting duck species including, most commonly, American Green-

winged Teal (*Anas crecca*), American Wigeon (*A. americana*), Mallard (*A.*

platyrhynchos), Northern Pintail (*A. acuta*), Canvasback (*Aythya valisineria*), Lesser

Scaup, Ring-necked Duck (*A. collaris*), Barrow's Goldeneye (*Bucephala islandica*),

Bufflehead (*B. albeola*), and Surf and White-winged Scoters. These duck species along

with their nests and ducklings, provide an important summer food resource for a host of

potential mammalian, avian, and fish predators including black bear (*Ursus americanus*),

lynx (*Lynx canadensis*), marten (*Martes Americana*), mink (*Mustela vison*), red fox

(*Vulpes vulpes*), red squirrel (*Tamiasciurus hudsonicus*), short-tailed weasel (*Mustela*

erminea), wolf (*Canis lupus*), Common Raven (*Corvus corax*), Great Gray Owl (*Strix*

nebulosa), Great-horned Owl (*Bubo virginianus*), Mew and Herring Gulls (*Larus canus*

and *L. argentatus*, respectively), and northern pike (*Esox lucius*; Lensink 1965, and D.

Safine pers. obs). More complete descriptions of the Yukon Flats are found in Lensink

(1965) and Heglund (1988 and 1992).

FIELD METHODS

Capture and monitoring of females. We captured White-winged Scoters by driving paired birds into floating mist nets (Kaiser et al. 1995) from 31 May to 13 June, 2002-2004. We captured birds at both Plot C and Scoter Lake Complex in 2002 but only at Scoter Lake Complex in 2003 and 2004. We marked females with stainless-steel U. S. Fish and Wildlife Service leg bands and individually numbered nasal disks (Lokemoen and Sharp 1985). We measured culmen, total tarsus, and head length to the nearest 0.1 mm (Dzubin and Cooch 1992) and body mass to the nearest 10 g. We outfitted females with prong and suture radio-transmitters (Mauser and Jarvis 1991, Pietz et al. 1995) modified with super glue (Model A4430, 9 g, 8 hour mortality switch, Advanced Telemetry Systems, Isanti, Minnesota). In 2004 we drew 1.5 cc blood samples to determine whether or not a female was producing eggs when captured. We transported blood in heparinized vacutainers, separated plasma from whole blood with a centrifuge, and froze the plasma within 12 hours. Blood samples were sent to Simon Frazer University to be analyzed for the circulating concentrations of the plasma yolk precursors vitellogenin (hereafter VTG) and very low-density lipoprotein (hereafter VLDL), using diagnostic kits for vitellogenic zinc (Zinc kit, Wako Chemicals) and total triglycerides (glycerol kit, Sigma), respectively. Levels of both VTG and VLDL serve as physiological indicators of reproductive state, and elevated levels of these yolk precursors identify hens undergoing either rapid follicle growth or producing eggs (Gorman 2005, Challenger et al. 2001). Samples were analyzed following the protocols of Mitchell and Carlisle (1991) and measured with a Biotel 340i microplate reader.

Females were tracked daily from the ground and once or twice weekly from a fixed wing aircraft until we either found their nests or confirmed them as failed or non-breeders, approximately 8 June – 8 July each year. During this intensive tracking period, we attempted to determine female status (paired or not paired), if on water, and nest location, if on land, without flushing the female. We only physically visited nests of radio-marked females during the initial visit and to determine hatch date in late incubation. From approximately 8 July – 25 August, we relocated all females once every two weeks from a fixed wing aircraft. We also tracked nesting and early brood-rearing (ducklings ≤ 14 days old) females every three days, and late brood-rearing females weekly from the ground.

Nest searching and monitoring. To increase our sample of scoter nests we conducted foot searches with the aid of a dog (Kehoe 1989), in addition to tracking hens marked with radio transmitters. We nest-searched lakeshores, islands, peninsulas, bog perimeters, and areas within 600 m of water from 8:00 to 16:00 Alaska Daylight Time, 21 June to 17 July, 2002 - 2004. We recorded data on nests of all duck species encountered during searches. We defined a nest as a depression with at least one duck egg that when revisited was either destroyed, had more eggs, or was being incubated. We did not include nests found destroyed or abandoned on our first visit in our analysis of nest survival. Nests abandoned due to researcher presence, which were very rare (N=1), were censored from the analysis after the last date known to be active.

At all nests we recorded: species (determined from egg size and color, down, contour feathers, or female; Bowman 2004); nest status (laying, incubating, hatched,

destroyed, or abandoned); incubation stage (determined from candling eggs; Weller

1956); habitat (from level I categories listed in the Alaska Vegetation Classification;

Viereck et al. 1992, Heglund 1992, and defined as the proportion of cover types in a 10 m

radius circle centered on the nest); and distance to water (defined as the shortest distance

to a lake). We recorded latitude and longitude for all nests with a compact Global

Positioning System (GPS) unit, and were able to revisit nests without any obvious

physical markers such as flagging, which might attract predators. We revisited nests at

approximately seven-day intervals for all non-radio-marked scoters and other duck

species, while the fate of nests of radio-marked scoters was determined every three days

by remotely locating those females from a lakeshore with telemetry equipment. Nests

were revisited until they hatched (at least one egg membrane), were destroyed by

predators (all eggs missing or destroyed, or some eggs missing or destroyed and

determined abandoned on a subsequent visit), or confirmed abandoned (at least two visits

with no change in incubation or number of eggs). Final visits were scheduled for one day

after predicted hatch date to count egg membranes.

Capture and monitoring of ducklings. We captured ducklings from nests and

newly hatched broods that appeared on the Scoter Lake Complex, 11 July – 1 August,

2003 and 2004. We caught hens and ducklings by hand or with long-handled landing

nets from nearly all monitored nests where eggs hatched. We monitored all boat-

accessible lakes in the study area every two days when ducklings began to appear (19

July – 1 August, 2003 and 2004), and attempted to catch the hen and a sample of the

ducklings from each newly hatched brood with floating mist nests (Kaiser et al. 1995)

modified for duckling capture. We marked, weighed, and measured hens as explained

above; however, we did not take blood samples, and previously marked females were

only weighed. We marked all ducklings in each brood with the same color code, one of

four colors of permanent marker applied to each white cheek patch (Eadie 1989, Schmidt

et al. 2005). In 2004, we also monitored a sample of unmarked ducklings with brood

hens that were nasal-marked in 2003, but not handled in 2004. We resighted ducklings

once every three days until ducklings were 14 days-old, then once every seven days until

ducklings were 30 days-old. We stopped monitoring survival past 30 days because most

duckling mortality occurs in the first 21 days (Eadie 1989, Traylor and Alisauskas 2005).

We typically resighted ducklings with 20-60x spotting scopes from shore. However,

broods were occasionally located too far from shore, and in this case were resighted with

10x binoculars from inflatable kayaks. Both approaches allowed us to identify marked

birds while minimizing disturbance. On each visit we recorded brood size, status (brood

amalgamation or not), number and color codes of marked individuals, location, duckling

age(s), and hen radio frequency or nasal disk number. All study protocols were approved

by the Institutional Animal Care and Use Committee at the University of Alaska

Fairbanks (IACUC #02-06).

STATISTICAL ANALYSIS

We estimated survival of females, nests, and ducklings with the nest survival model in

program MARK (White and Burnham 1999). The nest survival model is a form of

known fate models, which allows for unequal intervals between resightings (White and

Burnham 1999). Because resighting intervals varied from 2002 – 2004, estimating daily

survival rate (hereafter, DSR) with nest survival models was more interpretable than

interval-specific survival using known fate models. Nest survival models were used to

estimate duckling survival by Walker and Lindberg (2005) and Schmidt et al. (2005).

The nest survival model uses generalized linear models to obtain maximum likelihood

estimates of DSR, and we chose the logit or log-odds link function as it is the appropriate

link when analyzing binomial response data (Ramsey and Schafer 1997), such as

survival. The assumptions of our analyses were: fates of sampling units (nests or

individuals) are known with certainty, fates of sampling units are independent, lack of

heterogeneity in survival within strata, and survival is not influenced by observers or

markers (Williams et al. 2002, Dinsmore et al. 2002). The known fate assumption was

met for nests and cases where detection probability was < 1.0 for hens and ducklings are

discussed in individual sections below. The independence assumption was likely violated

for duckling survival, due to multiple marked ducklings in the same brood or crèche

(Korschgen et al. 1996, Hoekman et al. 2004), and potentially for nest survival, when

nests were located in close proximity, such as on islands or peninsulas (Walker et al.

2005). The heterogeneity assumption may have been violated for nests, ducklings, and

females as DSR likely varied within some strata, and we could not always account for

this extra-binomial variation with the covariates in our models (Dinsmore et al. 2002,

Williams et al. 2002). To account for possible violations of the independence and

heterogeneity assumptions (collectively called overdispersion), estimates of sampling

variance and model selection uncertainty can be adjusted with the variance inflation

factor $\hat{c}$. The variance inflation factor is frequently calculated as [deviance/deviance degrees of freedom] from the most parameterized (global) model (Burnham and Anderson 1998), where deviance is expected to be the smallest. However, this measure of overdispersion is known to be biased high (McCullagh and Nelder 1989). Furthermore, the nest survival model of Program MARK does not provide a method to obtain unbiased estimates of overdispersion (Dinsmore et al. 2002), so our primary inference was obtained from models unadjusted for overdispersion. We do however present how model selection and sampling variance changes when we adjusted for $\hat{c}$ estimated using the deviance/df. The last assumption, no observer or marker effects, is a concern in survival studies, and therefore we made every attempt to minimize disturbance to marked individuals and nests and use appropriate markers during the course of the study.

We chose sets of biologically relevant models, and selected among competing models with Akaike's Information Criteria (Akaike 1973) adjusted for small sample size (AIC$_c$; Burnham and Anderson 1998). We considered sources of variation present in all models within seven units of the best approximating model (ΔAIC$_c < 7$), but generated survival estimates from the most parsimonious model. Logit scale parameter estimates whose 95% confidence interval included zero were not considered in this analysis. We back-transformed logit-scale regression equations to get real DSR estimates, and period-specific survival was obtained by raising DSR estimates to the power of the period duration.

Female summer survival. Transmitter failure and emigration from the study area may have caused violations of the known fate assumption in this analysis (Williams et al. 2002). Therefore, we censored individuals once their fate was unknown, which is appropriate as long as censoring individuals is random and independent of fate (Williams et al. 2002). We minimized censorship by surveying a large area from the aircraft ($\geq$ 20 km from our field camp), and using long-life transmitters, which resisted destruction by large predators (D. Safine pers. obs.). We included the following covariates in the analysis to explain variation in hen survival: body mass, structural size, season day, and year. We converted body mass to a normal score, $z = \dfrac{x_i - \bar{x}}{\hat{\sigma}}$, using the mean and standard deviation of mass from the capture period, either prior to incubation or near hatch, that we sampled each bird. We used normalized total tarsus scores, calculated as above, as a structural size covariate because it was the only structural measurement taken that explained a significant amount of variation (β_{tarsus}=21.6 g*mm^{-1}, *F*=7.5, *P*=0.01) in body mass. The first day of the season was designated as May 31st and was converted to season day one in all years. Our candidate model set included 12 models with additive effects of up to four covariates, and we also examined a quadratic relationship with mass. We also included the null model, DSR (constant).

Nest survival. We included the following covariates in the analysis of nest survival: season day, season day^2, nest age, nest age^2, distance to water, distance to water^2, year, genus, and habitat type. Season day was calculated the same as above, and nest age was recorded as the average stage of incubation in the eggs on each day that a nest remained in the sample (Dinsmore et al. 2002), age of nests with fresh eggs were

recorded as zero until incubation began. Incubation periods (in days) of duck species in our sample were assumed to be as follows (Bellrose 1980, Afton and Paulus 1992, Brown and Brown 1981): Green-winged Teal (22), Northern Pintail (23), Canvasback (24), Mallard and American Wigeon (25), Lesser Scaup and Ring-necked Ducks (26), White-winged and Surf Scoters (28). The laying period for scoters was calculated as average clutch size*laying rate (1.0 egg*1.5 days^{-1}; Brown and Brown 1981). Our candidate model set for nest survival had 31 models, including additive effects with up to five covariates and the null model. We included two-way interactions among covariates and investigated quadratic trends in nest age, season day, and distance to water. All estimates of nest survival presented in this analysis are for White-winged Scoters unless otherwise noted. We generated estimates using the covariate values and nesting period for White-winged Scoters.

Duckling survival. Ducklings violated the known fate assumption when their color markers faded or if total brood loss or abandonment occurred in broods with a marked female but no marked ducklings. We did not observe total brood loss attributed to emigration from the surveyed lakes. Color markers lasted approximately three weeks, after which time high survival (Eadie 1989, Traylor and Alisauskas 2005, Walker and Lindberg 2005) and site fidelity (D. Safine pers. obs.) of ducklings allowed us to monitor fate by counting ducklings using established locations. In most cases, brood size was constant after three weeks of age. In 2003, all broods had marked ducklings, and 70% had marked hens, so unknown fate due to total brood loss or brood abandonment by females was not an issue. In 2004, our only violations of known fate were for marked

females with unmarked broods on the larger lakes, where the females were not resighted more than once with ducklings (*N*=3). Because we couldn't differentiate between females moving ducklings into a crèche and brood loss, we removed these unmarked broods of marked hens on the larger lakes from the analysis. We included the following covariates in the analysis to explain variation in duckling survival: duckling age, year, minimum daily temperature, daily precipitation, and wetland size. Duckling age was input in a similar fashion as nest age (Dinsmore et al. 2002, Schmidt et al. 2005): ducklings caught on the nest were recorded as 1 day-old, ducklings caught or first observed on the lake during their first week of life, class I A (Gallop and Marshall 1954, Bellrose 1980), were assumed to be 4 days-old, and ducklings first observed or captured in the second week of life, class I B, were assumed to be 11 days-old. Weather data came from Fort Yukon, Alaska, the nearest weather station available, and was recorded as a covariate for each day an individual remained in the sample. Wetland size was a categorical variable with two classes: a wetland that is part of, e.g. connected by water to, one of the two main lake systems in the study area, or a smaller wetland that was isolated from the main lake systems (Fig. 1). We divided the wetlands in this manner because Northern Pike and more gulls were observed in the larger lakes; therefore, we expected higher survival in the smaller wetlands. We did not incorporate female or duckling mass and structural measurements, which are commonly used in these analyses (Walker and Lindberg 2005, Schmidt et al. 2005, Traylor and Alisauskas 2005), because we did not handle all ducklings or hens. Our set of candidate models included 14 models with additive effects and two-way interactions. Models included up to five covariates with no

quadratic terms and the null model. Values reported in the results section are means ±

SE, unless otherwise noted.

RESULTS

Adult females. We captured and radio-marked a sample of paired female White-winged

Scoters from 31 May to 13 June in 2002 through 2004 (N=20, 25, and 34, respectively).

We also captured and radio-marked a sample of hens at hatch or with young ducklings

from 11 July to 1 August, 2003 and 2004 (N= 6 and 7, respectively). Mean body mass

differed between females captured prior to incubation (1527 ± 14 g) and those captured

with broods (1056 ± 14 g); thus, females lost on average 31% (470 ± 36 g) of their body

weight during the laying and incubation periods. We tracked radio-marked hens (N=92)

for a maximum of 55 days in 2002, 77 days in 2003, and 87 days in 2004.

The plasma yolk precursor analysis of females in 2004 (N=36) indicated egg-

producing (N=24) and non-egg-producing (N=12) females were present in our sample of

hens. Non-egg-producing was recorded if concentrations of VTG $\leq$ 1.4 μg*ml^{-1}and total

VLDL $\leq$ 5.1 mmol*l^{-1} (Gorman et al. 2005). Gorman et al. (2005) reported an error

misclassification rate of 13% using those cut-off values from both VTG and total VLDL

data. Intra-assay coefficients of variation were 7.2% for VTG using a laying hen plasma

pool (n = 15) and 8.3% for total VLDL using a 19-week hen plasma pool (n = 14). Inter-

assay coefficients of variation were 7.9% and 5.3% for VTG (n = 6) and total VLDL (n =

4), respectively. Subsequent telemetry locations of marked females led us to include two

more hens in the egg-producing category, totaling 72% (26 of 36 females) egg-producers

and 28% non-egg-producers, with VTG and VLDL concentrations separating these

groups (Fig. 2).

Of those 26 egg-producing females, nine had nests that survived to the onset of

incubation, and 65% had nests destroyed or abandoned during laying. Because we knew

onset of incubation and clutch size for some marked hens (N=7), we also know

approximately how many days prior to laying blood samples were taken. Blood

concentrations of yolk precursors exceeded cut-off values for those egg-producing

females up to 16 days prior to laying. We are therefore confident the proportion of non-

egg-producing females is close to the actual proportion of non-breeding females present

on the study area in 2004 rather than simply birds sampled too far in advance of laying.

Body mass of females was correlated with levels of VTG (r=0.68, P<0.0001, N=30) and

VLDL (s=0.49, P<0.01, N=36; Fig 3). Heavier females had higher levels of plasma yolk

precursors, and thus were more likely egg-producers. The average egg-producing female

weighed 1578 ± 20 g, 219 ± 37 g heavier than non-egg-producers which averaged 1359 ±

26 g. The heaviest non-egg-producer was 1480 g, whereas the lightest egg-producer was

1410 g, so some overlap occurred.

Female summer survival. Female mortalities during the laying and incubation

periods of 2002 - 2004 (1,3,and 6 respectively) were located at or near nests, or far from

the water in what appeared to be nesting habitat. The only mortality recorded outside the

nesting period (and near water) was that of one brood-rearing female killed in 2003. A

total of 11 mortalities was recorded, and known predators included black bear (*Ursus*

americanus), mink (*Mustela vison*), and owl (*Bubo virginianus* or *Strix nebulosa*). We

suspected red fox (*Vulpes vulpes*), lynx (*Lynx canadensis*), and wolf (*Canis lupus*) of

other hen mortalities. Of the ten females killed during the nesting season, five of those

hens were never visited on land prior to being found dead. Therefore, at least 50% of the

nesting mortalities occurred without the possibility of observer effects.

Nine models (Table 1) were within 7 AIC_c of the most parsimonious model,

DSR(mass). There was some evidence that season date, tarsus, and mass squared

explained variation in survival, but those parameters were not estimated to be different

from zero. Logit scale parameter estimates from the model DSR (mass), ($\beta_o = 6.20 \pm$

0.37, $\beta_{(body\ mass)} = -0.72 \pm 0.34$), indicate a negative effect of increasing body mass on

daily survival. Summer survival, for an 87 day period, of non-egg-producing females at

their mean mass was 0.93, 95 % CI (0.75, 0.98), whereas the survival rate of egg-

producing females at their mean mass was 0.79, 95% CI (0.65, 0.88; Fig 4). The variance

inflation factor was estimated at 1.39, indicating little overdispersion in the data.

However, this adjustment inflated the variance enough to make the 95% CI of the mass

parameter in the most parsimonious model, still DSR (mass), include zero. Therefore, if

we adjusted for overdispersion, we would estimate summer survival of females from the

constant DSR or null model (DSR= 0.997 ± 0.001), and summer survival probability at

0.80, 95% CI (0.64, 0.90). Estimates from the null model were very similar to those of

egg-producing females, and simply indicated that our sample consisted mainly of egg-

producing females.

Nest survival. During summers of 2002 – 2004 we located and monitored 27 scoter nests (which included 1 of a surf scoter), 16 dabbling duck nests (*Anas sp*.), and 23 pochard nests (*Aythya sp*.). Nest predators were likely similar to those listed for female White-winged Scoters above, except on pochard nests, especially Canvasbacks, which were probably destroyed most often by gulls (D. Safine pers. obs). Mean clutch size for scoters was 8.1 ± 0.2 eggs, and average laying date was 9 June each year (Table 2).

Four models were within 7 AIC_c of the best approximating model, DSR(season day+nest age+habitat; Table 3). The global model was the only one of the models within 7 ΔAIC_c that include the effects of year and genus; however, year and genus parameters have confidence intervals that include zero. The best approximating model was 3.8 AIC_c from the next best model and the parameters estimates were: $\beta_{forest\ habitat}$= 5.31, 95% CI (3.57, 7.05); $\beta_{(season\ day)}$= -0.10, 95% CI (-0.15, -0.04); $\beta_{(nest\ age)}$= 0.09, 95% CI (0.03, 0.16); $\beta_{(scrub\ habitat\ adjustment)}$= 0.24, 95% CI (-0.79, 1.27); $\beta_{(graminoid\ habitat\ adjustment)}$= -0.98, 95% CI (-1.76, -0.21), indicating that DSR decreased with season day and increased with nest age (Fig. 5); DSR do not differ in forest and scrub habitats, but survival was lower in graminoid habitat. Because the DSR (genus) model indicated that daily survival rate did not differ among genera of ducks present on the study area [$\beta_{(scoters)}$= 2.90, 95% CI (2.45, 3.36); $\beta_{(dabbling\ duck\ adjustment)}$= 0.38, 95% CI (-0.62, 1.38), $\beta_{(pochard\ adjustment)}$= -0.28, 95% CI (-0.96, 0.40)], we believe that estimating survival of scoters from a data set including multiple duck species is a valid approach to improve the precision of scoter nest survival estimates. We estimated nest survival during incubation (28 days) from the most parsimonious model on the mean laying date for scoters as 0.25, 95% CI (0.13, 0.49) in

forest (or scrub) habitat and 0.03, 95% CI (0.01, 0.16) in graminoid habitat. Survival for

both the laying and incubation period (40 days) was 0.18, 95% CI (0.08, 0.39) and 0.01,

95% CI (0.00, 0.07) in forest and graminoid habitat, respectively.

From the global model, $\hat{c}$ was estimated at 2.73, and both sampling variance and

model selection uncertainty increased substantially when we adjusted for overdispersion.

There were 28 models within 7 $QAIC_c$ of the best approximating model, DSR (constant),

and none of the logit scale slope parameters (year, nest age, season day, genus, distance

to water, or habitat type) had 95% CI different from zero. DSR from the constant

survival model adjusted for overdispersion was 0.946, 95% CI (0.912, 0.967); nest

survival probability during incubation (28 days) was 0.21, 95% CI (0.08, 0.39) and

survival for both laying and incubation period (40 days) was 0.11, 95% CI (0.03, 0.26).

Duckling survival. We determined the fates of both marked (*N*=88) and

unmarked (N=39) White-winged Scoter ducklings that belonged to a total of 21 broods

during the course of the study. In 2003, we marked and followed the fate of 57 ducklings

in ten broods, and in most (seven) cases we also radio-marked the female. In 2004, we

marked and followed fates of 31 ducklings in six broods and again marked most of the

brood hens (*N*=5). Additionally, we monitored a sample of 39 unmarked ducklings in

smaller wetlands accompanied by five females nasal-marked in 2003, but not handled in

2004.

There were two models within 7 AIC_c of the best approximating model, DSR

(minimum daily temperature + duckling age + year + wetland size; Table 4). All three

models include the effects of duckling age, year, and wetland size, the most parsimonious

model included temperature effects, and the global model added precipitation and interactive effects among covariates (year*duckling age, and minimum temperature*precipitation) to the most parsimonious model. The precipitation effects in the global model are poorly estimated due to lack of precipitation in 2004 [$\beta_{(precip)}$= -320.3, 95% CI (-1043.4, 402.8)], and the confidence intervals for year-specific duckling age parameters overlap [$\beta_{(duckling\ age\ 2003)}$= 0.21 % CI (0.10, 0.33) $\beta_{(duckling\ age\ 2004)}$= 0.12, 95% CI (0.04, 0.20)]. We estimated DSR from logit scale parameters in the top model, [β_o= 6.18, 95% CI (2.77, 9.59); $\beta_{(min\ daily\ temperature)}$= -8.45, 95% CI (-14.41, -2.50), $\beta_{(duckling\ age)}$= 0.16, 95% CI (0.10, 0.22); $\beta_{(2003\ adjustment)}$= -1.68, 95% CI (-2.35, -1.01); $\beta_{(wetland\ size)}$= 2.34, 95% CI (1.38, 3.30)]. DSR was lower in 2003, at the larger connected wetlands in the study area; it increased with duckling age, and decreased with temperature (Fig. 6). Survival probability to 30 days for ducklings hatching on the mean date in 2003, therefore experiencing daily temperatures from that day forward, at large wetlands was 0.01, 95% CI (0.00, 0.05) and small wetlands was 0.59, 95% CI (0.36, 0.96). In 2004, at large wetlands, ducklings hatched at the mean date survived at a rate of 0.33, 95% CI (0.20, 0.53), and 0.89, 95% CI (0.80, 1.00) at small wetlands. Average 30 day duckling survival rate in each year from the DSR (year) model was 0.08 95% CI (0.03, 0.15) and 0.64 95% CI (0.51, 0.75) in 2003 and 2004, respectively.   From the global model we estimated $\hat{c}$ = 1.92, and model selection results changed only slightly when we adjusted for overdispersion. The most parsimonious model remained the same, and confidence limits still differed from zero for all logit-scale parameters.

DISCUSSION

This is the first study on the breeding ecology of White-winged Scoters in Alaska and the northern boreal forest, and one of few studies that includes forest-nesting ducks. Additionally, we provide estimates of the proportion of egg-producing scoters on the breeding grounds; an estimate that approximates breeding probability. We estimated survival of nests, hens, and ducklings, and described sources of variation in these vital rates.

Breeding probability. Estimates of breeding probability are difficult to obtain and are potentially biased in wild birds, thus few estimates are available for comparison (Johnson et al. 1992, Sedinger et al. 2001). Hoekman et al. (2002) included a breeding probability estimate of 0.97 for Mallards, suggesting nearly all females attempted to nest. Guyn and Clark (2000) found 76% of radio-marked Northern Pintails attempted to nest, similar to the 72% we estimated from blood assays for White-winged Scoters. However, it is important to note detection probability of nesting pintails was almost certainly < 1.0 (McPherson et al. 2003) and therefore the proportion of female pintails that attempted to nest was likely higher than 76%. High renesting probability in dabbling ducks creates high numbers of observed nests per female (e.g. 1.41, seen in Mallards; McPherson et al. 2003). Because scoters have a low renesting propensity (Brown 1981, Traylor et al. 2004) and low detection of nests during laying, we observed only 0.26 nests per female at the Scoter Lake Complex. Thus, because scoters had similar nest survival (this study) but

lower breeding and renesting probabilities than dabblers, they must maintain higher annual or duckling survival than dabblers to maintain stable population levels.

The physiological approach we used to estimate breeding probability does not assume birds present on the breeding ground are nesting, and provides important evidence of non-breeding by birds that are paired and present on the breeding grounds. However, we could not address sources of variation in breeding probability with our sample.

The mark-recapture approach to determine the proportion of breeding birds in the population, not on the breeding grounds, provides important insights into factors that affect this vital rate. The most common factor is age, with younger birds having a lower probability of being present on the breeding grounds (Anderson et al. 2001, Sedinger et al. 2001). However, previous breeding experience, hatch date, and wetland conditions may also affect whether or not birds return to breeding areas (Viallefont et al. 1995, Anderson et al., Cam et al. 1998). It stands to reason that these same factors may also affect the breeding probability. We suggest that the non-egg-producing female scoters may be younger birds, e.g., two-year-olds, that migrate to the breeding grounds but do not breed until they return the following year at age three. Lifetime reproductive success may be adversely affected by the high cost of first breeding at age two (Viallefont et al. 1995). Non-egg-producing scoters may also be females that nested late in the previous year or who wintered in areas with low food availability, and did not reach a threshold mass needed for breeding. This may explain why only the heavier females were classified as breeders. Another hypothesis that explains the large proportion of non-egg-

producing females could be that scoters are not breeding periodically; a strategy that has been observed in kittiwakes and affected their survival and future breeding probability (Cam et al. 1998). This strategy was suggested in eiders observed to lay large clutches in the first year, small clutches in the second year, and which were hypothesized not to breed in the third year (Yoccoz et al. 2002). Nesting represents a significant source of mortality and possibly affects future reproductive output for female scoters. We suggest that scoters have a low breeding probability to ensure optimal body condition, and thus high reproductive output is most likely in years when females nest.

Prior to 2004, we did not have independent estimates of breeding probability based on blood assays. We suspected that radio transmitters reduced breeding probability or that nests were difficult to detect prior to the start of incubation and nests failed during laying. Our data from 2004 do not indicate that radio transmitters affect breeding of scoters. We radio-marked 34 White-winged Scoters in 2004. If we apply estimated nest survival during laying from the constant survival model [0.41; assuming 2.0 days per egg (D. Safine pers. obs.) or 0.51; assuming 1.5 days per egg (Brown and Brown 1981)] and a breeding probability of 72%, we would expect to detect 10 or 12 females on nests at the start of incubation. We observed nine females on their nest at the onset of incubation (when our detection probability for nests became high), which means we had 1-3 fewer females breeding than expected. We may attribute those missing hens to handling/transmitter effects, infrequent aerial telemetry flights during the early incubation period, or an overestimate of laying survival rate, as we have little data for the laying period. We believe a combination of the last two possibilities is the most likely

explanation, and that prong and suture radio transmitters do not negatively affect breeding females. If radios do negatively affect breeding, the effect size is likely small.

Female summer survival. The majority of mortality of scoter hens during the breeding season occurs during the laying and incubation period, and at this time the laying females are exposed to both avian and mammalian predators. We emphasize that nesting represents a significant source of mortality in the annual cycle of White-winged Scoter at the Scoter Lake Complex, and that female survival must remain quite high during the rest of the year to compensate for this mortality. Apparent annual survival for White-winged Scoters at Redberry Lake, Saskatchewan, ranged from 0.77 - 0.84 (Krementz et al. 1997, Alisauskas et al. 2004); thus our estimate of summer survival for egg-producing females (0.79) suggests that either scoters in Alaska have high non-breeding season survival or annual survival lower than that observed in Saskatchewan. We suggest that island-nesting scoters in Saskatchewan have higher summer survival and likely higher annual survival due to lower predator abundance on islands.

Walker and Lindberg (2005) estimated survival of brood-rearing female scaup at Minto Flats, Alaska at 0.80 95% CI (0.43, 0.95), indicating substantial mortality of females during brood rearing, a different pattern than we observed in scoters. The apparent survival estimate of nesting female scaup near Yellowknife, Northwest Territories was 0.80 ± 0.09 (42 day period), demonstrating high mortality for scaup in the boreal forest during nesting as well. Scaup appear to have higher mortality during the breeding season (especially brood rearing) and year (0.43; Rotella et al. 2003) than scoters, an unexpected pattern given the relatively open graminoid habitat they typically

use for nesting (Petrula 1994), and the dense, woody cover, used by nesting scoters that may be difficult to escape (Brown and Frederickson 1989, D. Safine pers. obs.). Nest and brood-rearing habitat used by scoters at the Scoter Lake Complex may confer some survival advantages over other sympatric duck species such as scaup.

Nest survival. White-winged Scoters at the Scoter Lake Complex tend to lay smaller clutches (8.1 versus 8.7 – 9.1 eggs), have higher egg hatchability (92% ± 2 versus 85% ± 3), and initiate and hatch nests earlier (about 9 days) than those in central Saskatchewan (Traylor et al. 2004). Scoters, a late nesting duck at all latitudes, may be required to nest slightly earlier at higher latitudes due to an earlier freeze up, and the relatively long period required for fledging (Brown and Fredrickson 1983).

While our DSR estimates can be applied to the 28-day incubation period or the 40-day nesting period, we caution against the use of DSR^{40} estimates as the majority of our monitoring data comes from the incubation period only. However, it is interesting to note that nest survival during laying estimated from blood assay and telemetry data (nine of 26 egg-producing hens, or 35% of nests survive laying period) is slightly lower than estimates predicted from the constant nest survival model (0.41 - 0.51). This is additional evidence of the positive effect of nest age on DSR. Similar nest age effects were also reported for scoters in Saskatchewan (Traylor et al. 2004) and plovers in Montana (Dinsmore et al. 2002). We note that nest survival varies slightly among duck species as their incubation periods differ. Scoters are incubating 6 days longer than Green-winged Teal, and thus teal incubation survival is 0.34 versus 0.25 in scoters. Nest and potentially female survival costs are associated with the prolonged nesting period of scoters.

Another cost of the prolonged nesting period is that DSR decreases over the season (this study), and late-hatching scoters, the last bird nests on the ground each summer, have reduced survival. Conversely, Walker et al. (2005) estimated DSR of nests to be higher later in the season in all but one year, so there is some indication that the effects of season day differ by year and location for ducks.

Nest survival of White-winged Scoters from the constant survival model during incubation at Redberry Lake in 2000 and 2001 was 0.55 (Traylor et al. 2004) compared to 0.21 from the constant survival model at Scoter Lake Complex, consistent with the comment by Traylor et al. (2004) that ducks nesting on islands would have higher survival than mainland-nesting birds. We stress that despite the less precise estimates, survival estimates from mainland sites may be more applicable to White-winged Scoters throughout most of their range. Grand (1995) estimated nest survival for dabbling ducks and pochards on the Yukon Flats at a site 75 km west of our study area, and found DSR[28] to range from 0.01 to 0.16 from 1989 – 1991. These estimates are slight lower than ours, and may represent habitat specific survival rates as Grand (1995) searched mostly meadow and scrub habitat while we searched mostly forested habitat. We found lower DSR in graminoid habitats, which were most frequently used by scaup and shovelers. Those two species were the most common ducks in Grand's (1995) study. Walker et al. (2005) also supported habitat specific DSR and did not support species-specific models. We suggest that the ability of predators to detect nests varies by habitat, but predators locate different species with the same probability within a particular habitat type.

Duckling survival. Duckling survival was higher at smaller, isolated lakes in the study area. These smaller lakes did not appear to have Northern Pike and we observed gulls less frequently. Larger lakes were deeper, had longer reaches, and produced larger waves during wind events. Gulls have been noted as major duckling predators in numerous studies (Brown and Frederickson 1989, Traylor and Alisauskas 2005, Walker and Lindberg 2005). Traylor and Alisauskas (2005) estimated duckling survival between 0.00 and 0.01 for White-winged Scoters in Saskatchewan, drastically lower than our average estimates. If the effect of wetland size applies on a larger geographic scale, then Redberry Lake at 4500 ha (Traylor et al. 2004) may represent one extreme in wetland size, whereas some of the smaller lakes on our study site, where survival probability was 0.89 in 2004, would be the other extreme. Supporting this idea, Schmidt et al. (2005) estimated duckling survival of Common Goldeneyes between 0.64 – 0.67 at small, forested wetlands in interior Alaska. Duckling age had a positive effect on DSR as observed in many studies (Grand and Flint 1996, Traylor and Alisauskas 2005, Walker and Lindberg 2005), and DSR became nearly constant between about 10 and 20 days in both years and locations (Fig 5). Duckling survival not only varied by year, but also fluctuated in a similar pattern to another boreal forest study site (this study, Walker and Lindberg 2005). Walker and Lindberg (2005) estimated lower scaup duckling survival in 2003 (0.03) than 2002 (0.24), and we observed the same pattern at our study site 185 km northeast of theirs (peak scoter duckling count: 33 in 2003 and 234 in 2002). The factors affecting duckling production may be operating across species at a large spatial scale. Brook et al. (2005) describe a positive correlation between rodent abundance and scaup

productivity, and suggest that synchrony of small mammal cycles across a large geographic area may drive boreal duck productivity.

This study suggests that boreal forest White-winged Scoters have lower nest and breeding season survival, but higher duckling survival than scoters nesting in the prairie-parkland ecotone in Saskatchewan. Because nest and breeding season survival are the vital rates with the largest effects on population growth rate (λ; Hoekman et al. 2002), we believe high non-breeding season survival is important in maintaining stable scoter populations. Therefore, understanding factors that affect survival during the non-breeding season, such as habitat degradation and contaminants on the wintering grounds, should be important management goals.

In conclusion, we recommend that future studies of White-winged Scoters focus on estimating annual survival probability of females in order to understand what proportion of annual mortality occurs during nesting and brood rearing. Estimating annual scoter harvest would determine if consumptive use of scoters is an important source of mortality outside the breeding season. We recommend monitoring of sport and subsistence harvest, and implementation of sex-specific hunting regulations if harvest is deemed to be an important source of mortality. Studies that link conditions on the wintering grounds, age, female body condition, and prior breeding experience with breeding probability will be useful in understanding the low observed proportion of breeding females on the breeding grounds.

AKNOWLEDGEMENTS

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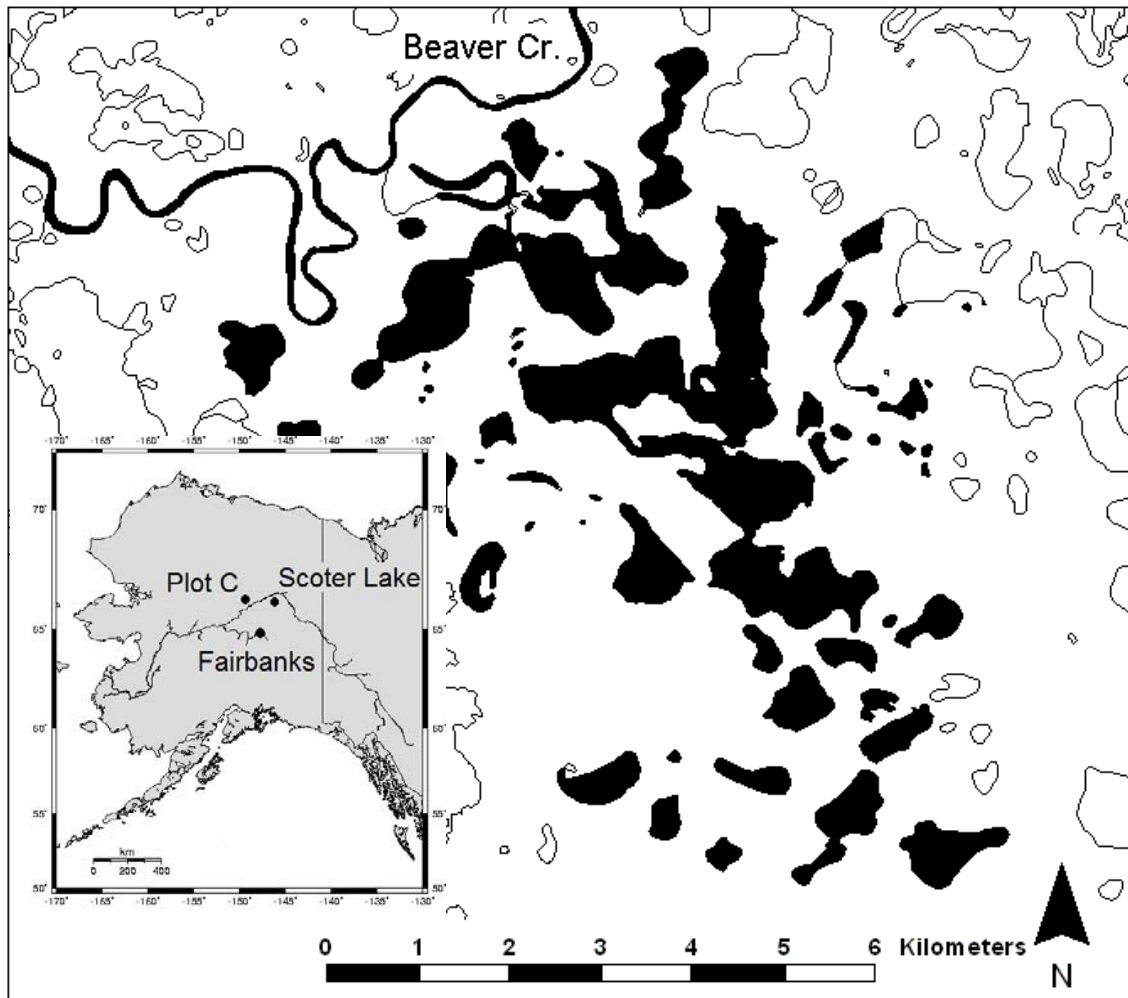
FIGURE 1. Features of Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska. Black waterbodies are the extent of study area visited from 2002 - 2004. Inset shows location of Scoter Lake Complex, Plot C, and Fairbanks, Alaska.
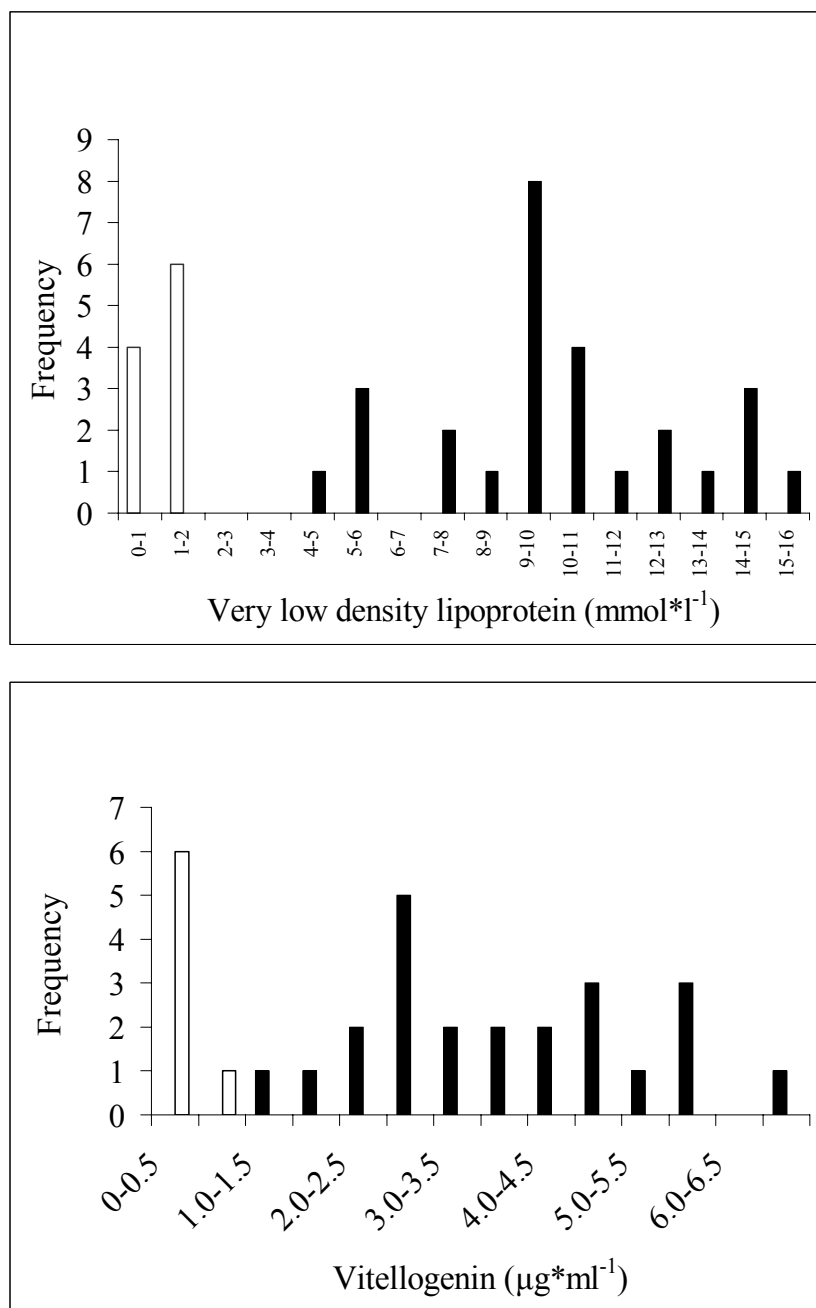
FIGURE 2. Frequency of female White-winged Scoters with various levels of the plasma yolk precursors vitellogenin (*N*=30) and very low density lipoprotein (*N*=36) at Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2004. White bars and black bars are females classified as egg-producers and non-egg-producers, respectively.
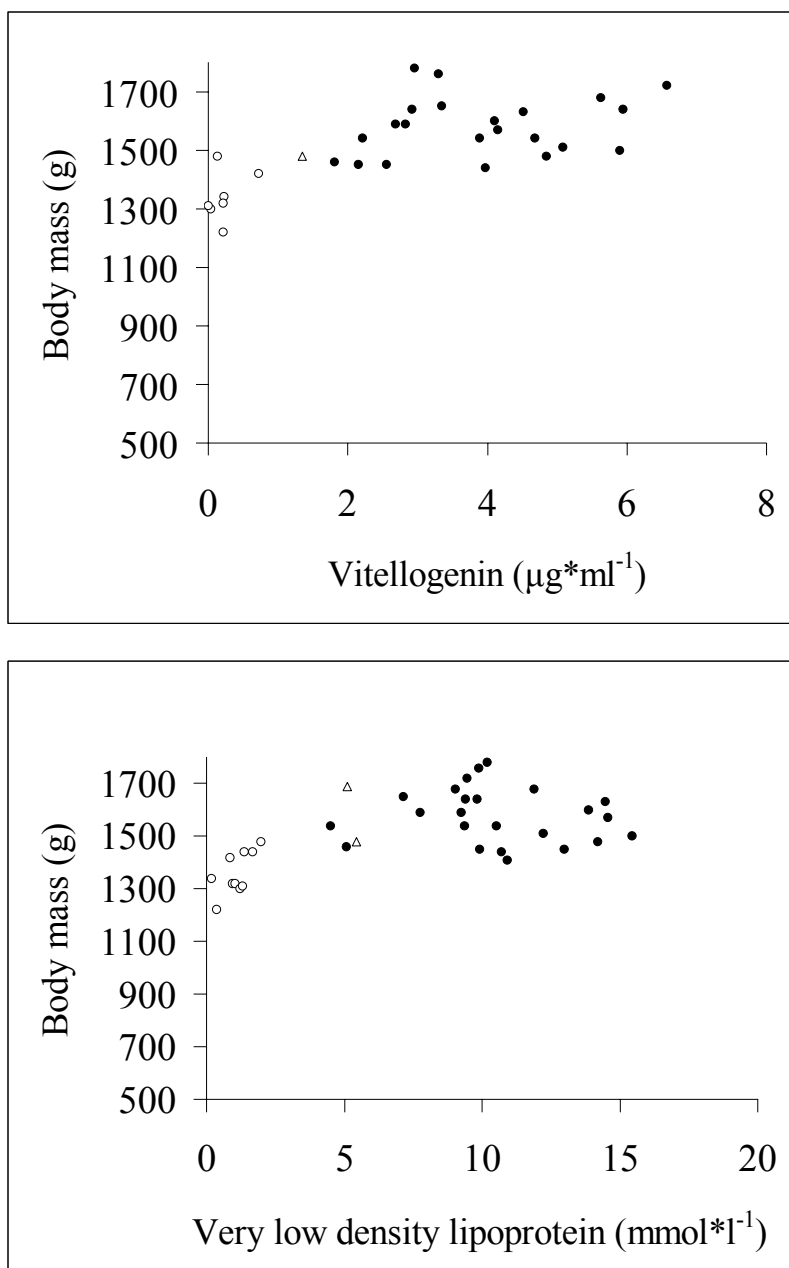
FIGURE 3. Relationship between plasma yolk precursor level and body mass of White-winged Scoters at the Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2004. White circles and black circles are females classified as non-egg-producers and egg-producers, respectively, white triangles are females misclassified as non-egg-producers, then re-classified as egg-producers from telemetry observations.
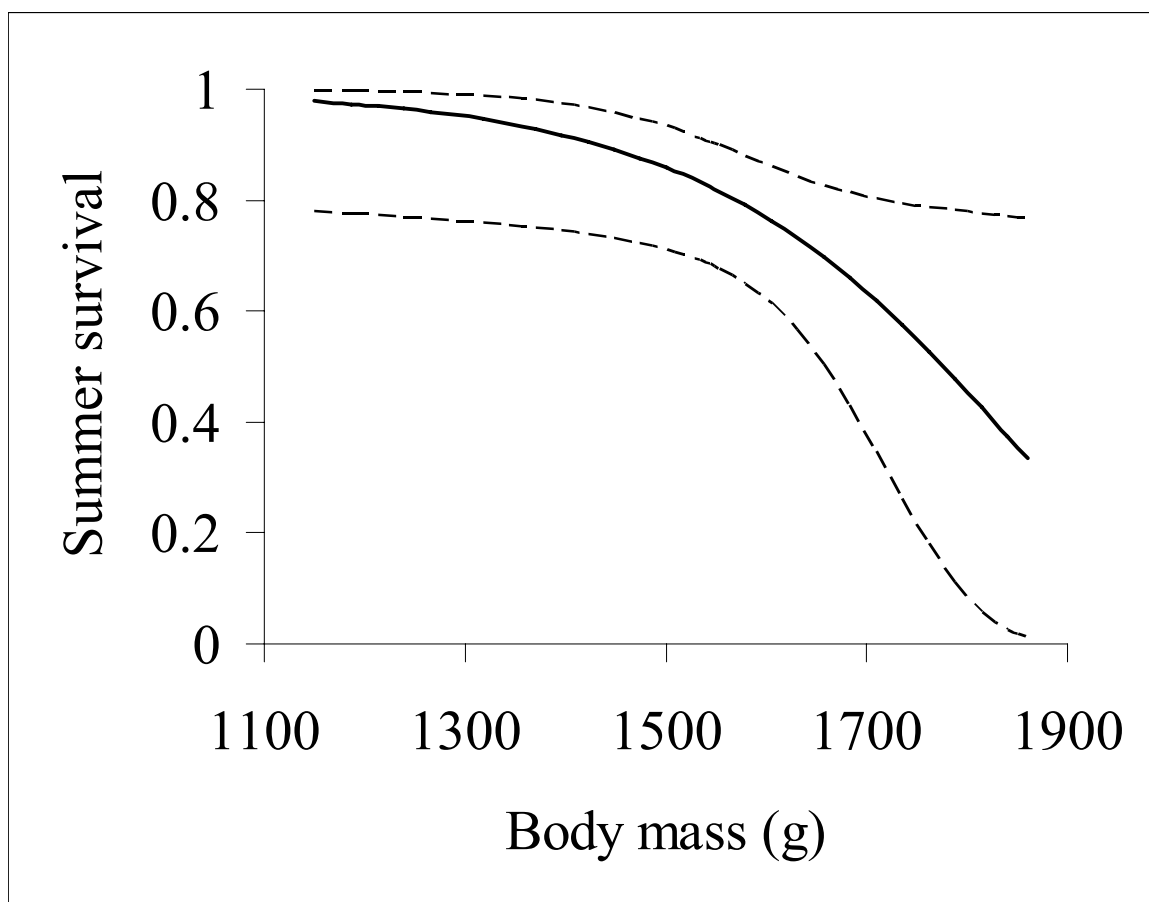
FIGURE 4. Relationship between summer survival probability of female White-winged Scoters and body mass upon capture at Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2002-2004. Survival probability is estimated for an 87 day period, dashed lines represent the upper and lower bounds of the 95% confidence limit.
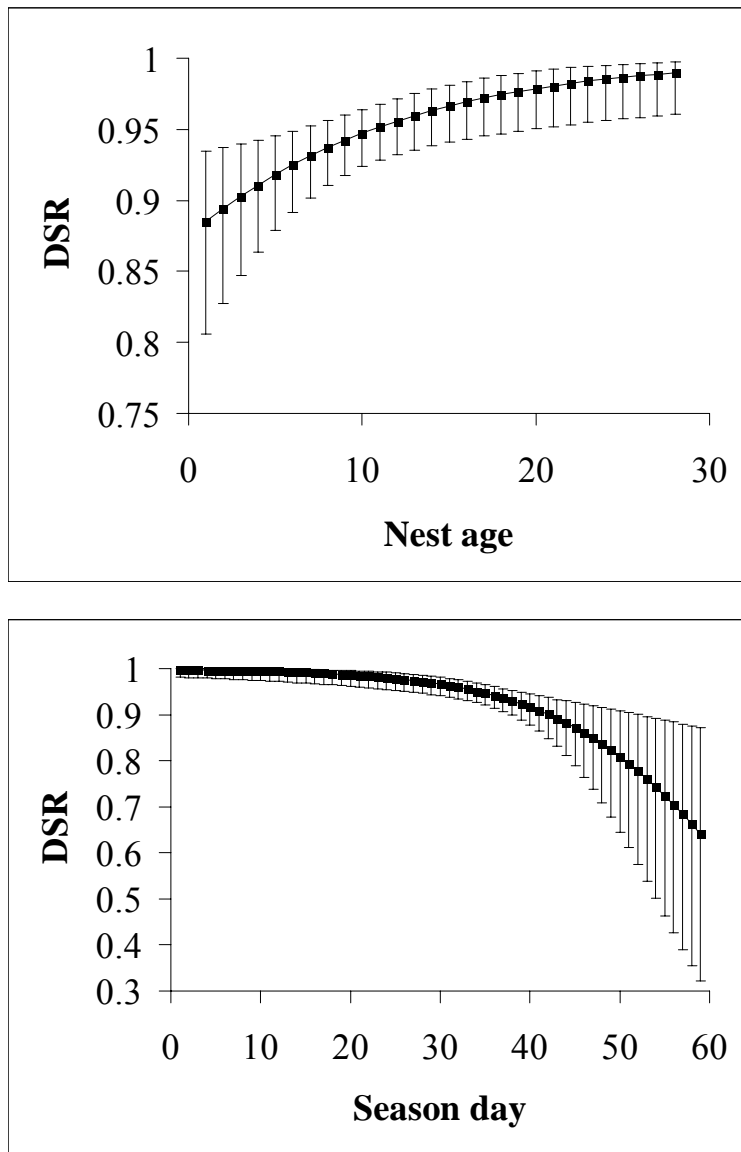
FIGURE 5. Relationship between White-winged Scoter daily survival rate (DSR) of nests, nest age, and season day at Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2003 - 2004. Error bars are 95% confidence intervals, nest age is equivalent to day of incubation, and 30 May is standardized as season day 0 in all years. Estimates of DSR are from the most parsimonious model at median season day or nest age.
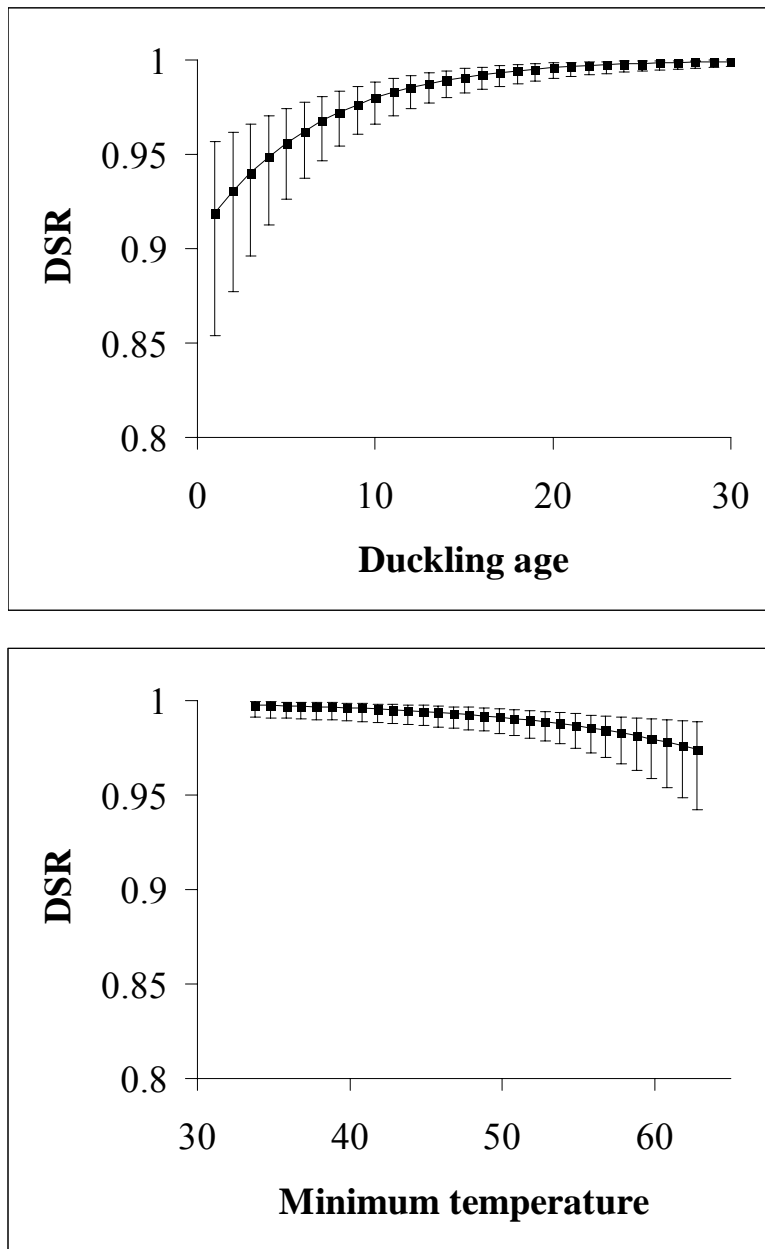
FIGURE 6. Relationship between daily survival rate (DSR) of White-winged Scoter ducklings and duckling age and minimum daily temperature at Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2003 - 2004. Error bars are 95% confidence intervals; estimates of DSR are from the most parsimonious model at mean minimum temperature or median duckling age, and averaged over year and wetland size.

TABLE 1. Selection results for models of adult female summer daily survival rate (DSR)
at the Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2002-2004.
Results are based on Akaike's information criterion, adjusted for small sample size
(AIC_c), and "+" symbols indicating additive relationships among parameters.

| Model	k^a	$-2log(l)^b$	AICc	ΔAICc^c	AICc weight[d]
DSR(mass)	2	120.7	124.7	0.0	0.31
DSR(mass+mass^2)	3	119.4	125.6	0.8	0.20
DSR(mass+tarsus)	3	120.6	126.7	2.0	0.11
DSR(season day[e]+mass)	3	120.6	126.7	2.0	0.11
DSR(constant)	1	125.3	127.3	2.6	0.08
DSR(year+mass)	4	120.1	128.4	3.6	0.05
DSR(season day+mass+tarsus)	4	120.5	128.7	4.0	0.04
DSR(season day)	2	125.2	129.3	4.5	0.03
DSR(year+mass+mass^2)	5	119.1	129.4	4.7	0.03
DSR(year)	3	124.9	131.0	6.3	0.01
Global: DSR(year+season day+mass+tarsus)	6	119.9	132.4	7.7	0.01

[a] Number of parameters.

[b] Maximized -2(log likelihood) value.

[c] Difference in AICc relative to the most parsimonious model.

[d] Estimated probability that each model is best for the data (Burnham and Anderson 1998).

[e] Logit scale linear trend of season day

TABLE 2. Mean clutch size, egg hatchability, nest initiation, onset of incubation, and

hatch dates (SE) for White-winged Scoters breeding at the Scoter Lake Complex, Yukon

Flats National Wildlife Refuge, Alaska, 2002-2004.

	Clutch size	Hatchability (%)	Nest initiation[a]	Nest initiation[b]	Incubation	Hatch
Mean (SE)	8.1 (0.2)	92 (2)	7 June (1.3)	11 June (1.3)	24 June (1.1)	22 July (1.1)
Range	7-10	86-100	26 May-18 June	30 May-21 June	13 June-2 July	11 July-30 July
n	23	8	22	22	26	26

[a] Nest initiation based on laying rate of 2 days per egg.

[b] Nest initiation based on laying rate of 1.5 days per egg.

TABLE 3. Selection results for models of daily nest survival rate (DSR) at the Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2002-2004. Results are based on Akaike's information criterion, adjusted for small sample size, (AIC_c); "+" and "*" symbols indicating additive and interactive relationships among parameters, respectively.

Model	k^a	$-2log\,(l\,)^b$	AICc	ΔAICc[c]	AICc weight[d]
DSR(season day[e]+nest age+habitat)	5	161.5	172.1	0.0	0.63
DSR(season day+nest age)	3	169.6	175.8	3.8	0.09
DSR(season day+habitat)	4	169.0	177.4	5.4	0.04
DSR(season day*nest age)	4	169.5	177.9	5.8	0.03
Global: DSR(season day+nest age+habitat+year+genus)	8	161.0	178.4	6.4	0.03

[a] Number of parameters.

[b] Maximized -2(log likelihood) value.

[c] Difference in AICc relative to the most parsimonious model.

[d] Estimated probability that each model is best for the data (Burnham and Anderson 1998).

[e] Logit scale linear trend of season day

TABLE 4. Selection results for models of duckling daily survival rate (DSR) at the Scoter Lake Complex, Yukon Flats National Wildlife Refuge, Alaska, 2002-2004. Results are based on Akaike's information criterion, adjusted for small sample size (ΔAIC_c), "+" and "*" symbols indicating additive and interactive relationships among parameters, respectively. Minimum daily temperature (min temp) and daily precipitation (precip) values were included in some models.

Model	k^a	$-2log(l)^b$	$AICc$	$\Delta AICc^c$	$AICc$ weight^d
DSR(min temp+duckling age+year+wetland size)	5	251.8	262.0	0.0	0.72
Global: DSR(precip*min temp+duckling age*year+wetland size)	8	247.6	264.3	2.2	0.24
DSR(duckling age+year+wetland size)	4	259.5	267.6	5.6	0.04

[a] Number of parameters.

[b] maximized -2(log likelihood) value.

[c] Difference in AICc relative to the most parsimonious model.

[d] estimated probability that each model is best for the data (Burnham and Anderson 1998).

CONCLUSION

The study is the first description of breeding White-winged Scoters in the northern boreal forest of Alaska, and the only to sample mainland nesting scoters throughout their range. This information was not previously available due to the challenges of collecting data on birds nesting in a dispersed pattern in very dense cover. I estimated important vital rates and described patterns of nest habitat use effectively at the Scoter Lake Complex, but I lack replicate study sites to determine whether our estimates are representative of interior Alaska, or more generally, the northern boreal forest. In fact, my study site was selected because it supported some of the highest densities of breeding pairs on the Yukon Flats National Wildlife Refuge, and a study here would be more logistically feasible than elsewhere. A concurrent study of breeding White-winged Scoter ecology is being conducted near Inuvik, Northwest Territories, Canada, by Ducks Unlimited Canada and collaborative efforts in data analysis may allow a much larger frame of inference for boreal scoters.

The most important findings in the first chapter helped explain why nest searching for White-winged Scoters was so inefficient. At the scale of my study area, scoters were selecting woody plant communities nearly at random. The only evidence of selectivity was their avoidance of non-woody or graminoid sites, otherwise use was proportional to availability. Because no plant communities were clearly preferred, finding a scoter nest was more likely due to random chance than a search effort in "good" nest habitat. This pattern of random nest site use may cause nest predators to focus on other waterfowl

species that can be located more readily, like scaup, which regularly nest much closer to water. However, scoters did show patterns of selection at a smaller scale. Within the habitats selected for nesting, scoters sought sites with more abundant and variable cover, and locations closer to edge and water than random sites. Dense cover may improve nest survival, while cover variability may form escape openings in the cover so these large sea ducks can fly from nests. Similarly, nesting close to edge, especially an edge type with lower cover, like a graminoid meadow, may further increase the chance female will survive the nesting period. Even though females were recorded nesting up to 725 m from water, most females were nesting closer to water than random sites. Nesting farther from lake shores, and known travel routes for nest predators, may improve nest survival, but requires ducklings to travel longer distances overland to reach the safety of lakes. In the second chapter, we found that duck nests in forested and scrub sites had higher survival than those in graminoid sites, and graminoid sites on the study area were often closer to water and offered less dense cover than forested or scrub communities. This provides evidence that scoter nest sites, which have more cover and are farther from water than most other sympatric duck species, offer relatively high nest survival rates.

High nest survival observed in the forested sites commonly used by scoters has associated costs to hens. In the second chapter we estimated high rates of female mortality during the breeding season associated with nesting. Our estimate of female breeding season survival was very similar to previous estimates of annual survival, indicating a large proportion of the annual mortality occurs during nesting. Female scoters nest in sites that are difficult for predators to locate, but are also difficult to flee.

Because the physiological approach separated egg-producing and non-egg-producing females, I determined that egg-producing females were substantially heavier, and that these heavier females had lower rates of survival during the summer period, more evidence that nesting is an important source of the mortality of White-winged Scoters.

In the plasma yolk precursor analysis, I found a correlation between body mass and breeding status, and suggesting females below a certain threshold of mass may not be able to breed. Females below this threshold may be younger, may have wintered in areas with poor food resources, or may have bred in the previous year. I estimated up to 28% of the paired females present on the study site did not attempt to breed in 2004. This proportion is important to consider in management because estimates of the breeding population size from U.S Fish and Wildlife Service surveys may include a large proportion of non-breeding individuals in a given year.

I estimated nest survival rates of White-winged Scoters to be similar to other species of boreal forest ducks, but lower than those of White-winged Scoters in Saskatchewan. I found daily survival rate of nests to increase over the incubation period, and decrease over the nesting season. Scoters, late nesters, had lower nest survival at the end of their long nesting season, and also had lower nest survival compared to other duck species simply because of their longer laying and incubation periods. The extended nesting period of scoters, 40 days on average, as compared to many dabbling ducks, 31 – 35 days, may cause scoters to nest more commonly in forested sites to offset the lower nest survival over this longer period.

Though boreal scoters appear to have lower nest survival than scoters in the prairie-parkland, I estimated duckling survival to be higher on the Yukon Flats. Traylor and Alisauskas (2005) found duckling survival to be no higher than 0.01, while we observed survival up to 0.33 on large wetlands, and 0.89 on small wetlands. Large wetlands have lower duckling survival rates as gulls and Northern Pike are more common at these lakes. Higher duckling survival may be one advantage of nesting in the northern boreal forest, but because nest survival appears to be more important in driving λ, this increased duckling survival may not be enough to offset low nesting survival.

The vital rates estimated and habitat selection patterns described in this thesis allow comparisons of these White-winged Scoters to those in the southern portion of the breeding range. They also indicate important areas for future research. I would recommend that future studies focus on estimating annual survival probability of females in the northern boreal forest, estimating breeding probability and sources of variation in this parameter, and estimating scoter harvest. Annual survival estimates will allow managers to determine whether female survival differs by latitude, and what proportion of the annual mortality may be attributed to nesting. Sources of mortality outside the breeding season, such as scoter harvest and oil spills, would be useful to estimate and consider in management plans. Because I estimated high female mortality during the nesting season, non-breeding season survival must remain high to maintain stable populations. I recommend monitoring of both sport and subsistence harvest, to determine whether these are important sources of mortality. Studies that link conditions on the wintering grounds, age, female body condition, and prior breeding experience with

breeding probability will be useful in understanding factors contributing to low breeding probability of females present on the breeding grounds. Managers must note that the actual number of breeding scoters each year is likely smaller than what has been estimated from breeding population surveys.

In conclusion, I found White-winged Scoters behaved counter-intuitively to my expectations, given previous experiences with other large sea ducks, such as eiders. Scoters appear to seek nest sites that offer higher nest survival, but significant risks to females. Because boreal forest predators are known fluctuate through time with small mammal populations (Brook et al. 2005), and I believe that the nesting strategy of scoters may be effective in years of low predator abundance. A reduced breeding probability may allow scoters to live long enough to breed in one or two of these high reproductive output years, and therefore benefit from their otherwise costly, in terms of high female mortality, nesting strategy.

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